THE OSTEOLOGY AND RELATIONSHIPS OF THE DENTICIPITIDAE, A FAMILY OF CLUPEOMORPH FISHES

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INTRODUCTION

THE family Denticipitidae was erected by Clausen (1959) for *Denticeps clupeoides*, a a peculiar little herring-like fish which he collected in a few streams in southwest Nigeria. As the name implies, the fishes have small, denticle-like structures on the dermal skull bones, an unusual feature in teleosts. But, the denticipitids show many other peculiar characteristics besides the dermal denticles, and Clausen suggested a number of possible affinities for the family; of these a clupeoid relationship seemed the most probable (Clausen, *op. cit.*).

While Clausen was working on Nigerian material I was puzzling over an unusual fossil fish from presumed Tertiary deposits at Singida, Tanzania (East Africa). With the publication of Clausen's paper, it was immediately apparent that the

fossils should be referred to the Denticipitidae. Indeed, the fossils differed only slightly from the extant west african form (Greenwood, 1960).

The fossil denticipitid (*Palaeodenticeps*) did not throw any more light on the phyletic relationships of the family. This question was considered by Rosen, Weitzman, Myers and myself (Greenwood *et al.*, 1966). At that time it became obvious that a detailed study of the Denticipitidae would be necessary to establish its inter- and intragroup relationships. However, from the evidence before us we concluded that the Denticipitidae constitutes a group of subordinal status within the superorder Clupeomorpha.

The present paper is an elaboration of the osteological and some other anatomical studies made in connection with our phyletic review. It is based on a greater number of specimens than were then available, and includes observations on skeletal systems which we could not then examine.

I feel incapable of adequately expressing my gratitude to Dr. Stenholt Clausen who so graciously allowed me to carry out this work on a family in which he has a very great personal interest. The information and specimens he so freely provided have been of inestimable value.

Material and methods. Most of the work is based on three alizarin transparencies prepared from the following specimens:

   (i)   B.M. (N.H.) reg. no. 1963. 12.11.6., 33 mm. standard length
   (ii)   B.M. (N.H.) reg. no. 1962. 5.17.7., 35 mm. S.L.
   (iii) B.M. (N.H.) reg. no. 1962. 5.17.8., 34 mm. S.L.

Supplementary information was obtained by dissection and from radiographs. All drawings were made with the aid of a camera lucida.

ABBREVIATIONS USED IN FIGURES

A_1; A_2	posterior openings to *recessus lateralis*	C_5	fifth ceratobranchial (lower pharyngeal bone)
AF	articular facet for first vertebra	CH	ceratohyal
Aob	antorbital	Cl	cleithrum
ART	articular	COR	coracoid
ASBoc	articular surface on basioccipital	cart	cartilage
ASEo	articular surface on exoccipital		
ASV	articular surface on first vertebra	D	dentary
af	auditory fenestra	DIM	dorsal intermuscular bone
ahf	anterior facet for hyomandibula	DR	distal pectoral radials
ang	retroarticular	Dsp	dermosphenotic
as	articular surface on the palatine (contacting ethmoid)	dHH	dorsal hypohyal
		dopc	dorsal opening of main preopercular laterosensory canal
B_{1-3}	first to third basibranchials	E	median ethmoid bloc
BH	basihyal	E_{1-4}	First to fourth epibranchials
Boc	basioccipital	ECT	ectopterygoid
Bs	basisphenoid	EH	epihyal
b_{1-5}	branchiostegal rays	ENT	entopterygoid
		Ep	epural
C_{1-4}	first to fourth ceratobranchials	Epi	epiotic

EX   extrascapular
Exo   exoccipital

Fbo   oblique frontal bridge
Fbs   parasagittal frontal bridge
FM   *foramen magnum*
FR   " floating " ribs
Fr   frontal
Fri   ridge on frontal
Fro   supraorbital ledge of frontal
Frs   pectoral fin rays
Frt   temporal flange of frontal
f   foramen for internal carotid artery

Gr   groove leading to supraorbital laterosensory area
gasc   groove for anterior semicircular canal

H1–3   first to third hypobranchials
H₁–H₃   first to third hypurals
Hmd   hyomandibula
HS   haemal spine
hsc   horizontal semicircular canal

INF   infundibular foramen
IOP   interoperculum
ihy   interhyal
ioc   opening for infraorbital latero-sensory canal into *recessus lateralis*
LE   Lateral ethmoid
LJ   lateral wall of the *pars jugularis*
lopoc   lower opening of the preopercular laterosensory canal

MC   mesocoracoid
ME   mesethmoid
MET   metapterygoid
MS   median septum of basioccipital
Mx   maxilla
mc   Meckel's cartilage

N   nasal
NaU   reduced neural arch of 1st ural vertebra
Nlm   nasal lamina

Obs   orbitosphenoid
OP   operculum
ORL   opening into *recessus lateralis* for preopercular and infraorbital laterosensory canals

OSB   foramen for swimbladder diverticulum
OSBD   opening for swimbladder duct
O and ö   anterior and posterior openings respectively for the horizontal semicircular canal

P   parietal
P1–4   first to fourth infrapharyngobranchials
Pa   parasphenoid
PAL   palatine
PE   *planum ethmoidale*
PF   facet for articulation with the palatine
PG   pelvic girdle
Pmx   premaxilla
POP   preoperculum
POPs   preopercular spine
Pp   pelvic plate
PR   proximal pectoral radials
Pro   prootic
PROB   prootic bulla
Psp   procurrent " spines "
Pter; Ptr   pterotic
Ptm   posttemporal
Pts   pterosphenoid
phf   posterior facet for hyomandibula
poc   opening for preopercular laterosensory canal into *recessus lateralis*
popg   groove on preoperculum leading to main laterosensory canal

Q   quadrate

rFr   pelvic radials
rPp   radial for pelvic plate

SBD   bony eminence surrounding the opening for the swimbladder duct
SC   scapula
So   supraorbital
Soc   supraoccipital
SOP   suboperculum
Sph   autosphenotic
SR   saccular recess
SYM   symplectic
sa   sesamoid articular

tf   temporal foramen

U1–U2	first and second ural vertebrae	vHH	ventral hypohyal
UF	utricular foramen	X	anterior ridge on prootic
UN	uroneural		
uopoc	upper opening to the main pre-	1–5	first to fifth infraorbital bones
	opercular laterosensory canal	1st C	first principal caudal ray
		1st PR	first pleural rib
V	vomer	III	passage for oculomotor nerve
V_1	first vertebra	IX + X	foramen for glossopharyngeal
VIM	ventral intermuscular bone		and vagus nerves

THE OSTEOLOGY OF *DENTICEPS CLUPEOIDES* CLAUSEN, 1959

The Syncranium

An outstanding feature of the skull in denticipitids is the occurrence of odontodes (Orvig, 1967) on at least part of the exposed surfaces of all dermal bones (see Text-fig. 1; also Clausen, 1959, fig. 1, and Greenwood, 1960, fig. 1, and pl. 2). The odontodes are of different form, varying from long and slender to short and stout variants of a basically conical shape. Their distribution patterns on the bones, and their density, appear to be constant in all the specimens examined. Since most of the frontals lie below and well separated from the skin (see below), the dorsicranium shows a relative absence of odontodes, which are confined to a patch on the temporal region and a prominent line above the eye. The jaws, cheeks and opercular region are densely " toothed " and give the ventral half of the head a decidedly " furred " appearance.
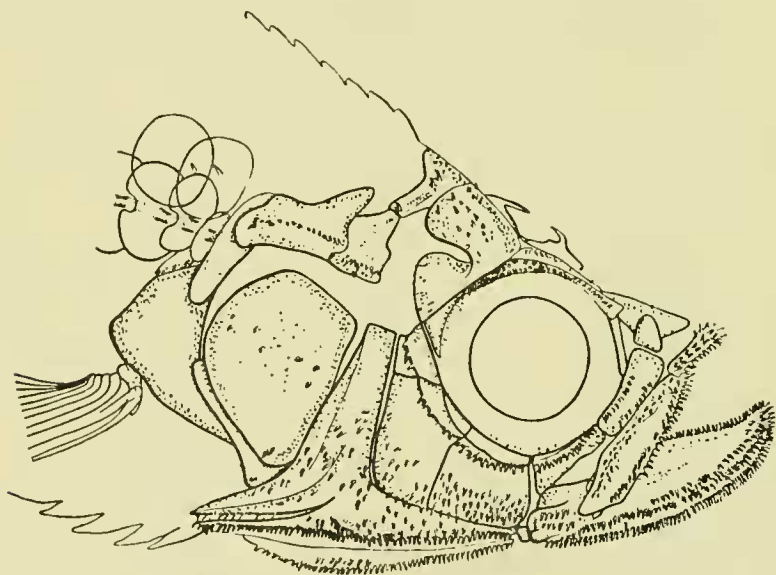

FIG. 1. *Denticeps clupeoides*; syncranium in lateral view to show distribution of odontodes. Modified after Clausen(1959).

Odontodes occur on the extrascapular and posttemporal bones, but are restricted to a single row following the course of the laterosensory tubes. A similar condition is found on the parietal.

The neurocranium of *Denticeps clupeoides* (Text-fig. 6) also has a characteristic appearance, smoothly contoured, and markedly inflated in the otico-occipital region. In dorsal view it has an almost rectangular outline, with a slight narrowing of the anterior half (see Text-fig. 3). The dorsal surface is entire since neither frontal fontanelles nor pre-epiotic fossae are present. The large, gutter-like nasals, together forming a U-shaped structure, lie above the level of the skull roof. The dorsal surface is further broken by the two bony bridges crossing the orbital region of each frontal (Text-figs. 3 and 5). In the transverse plane, the neurocranium is almost circular, its contours broken ventrally by the prominent bulge of the prootic bullae, and the small auditory fenestrae.

Olfactory region. (Text-figs. 2, 3, 5 and 6.) The ethmoid bloc is short, and dominated by its large lateral wings (Text-figs. 2 and 3). Judging from the pattern
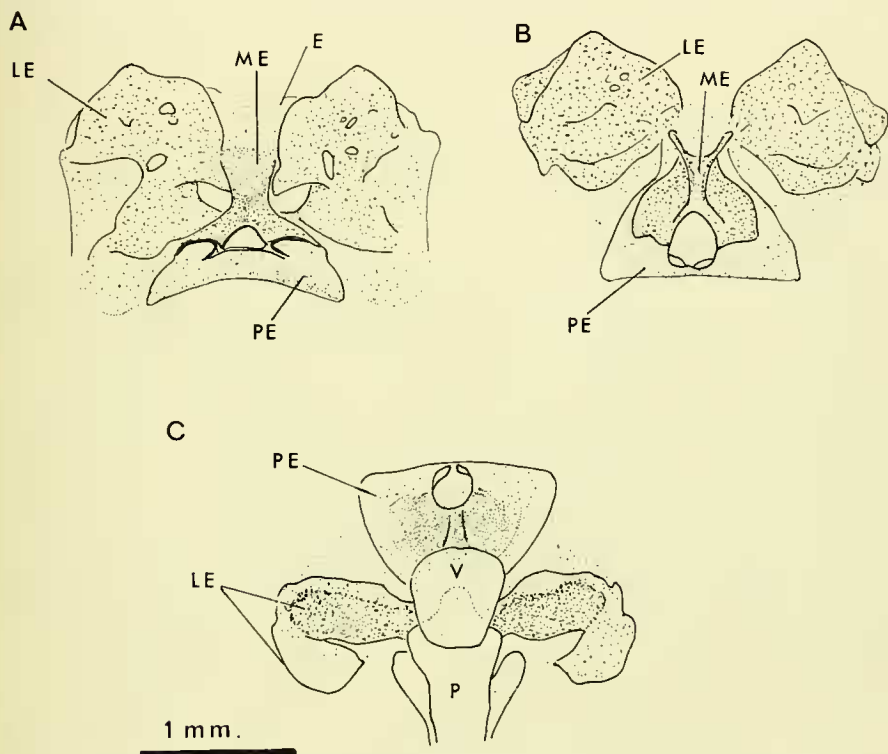

FIG. 2. Ethmoid bloc. (A) Anterior view. (B) Dorsal view, long axis aligned horizontally. (C) Ventral view, the long axis aligned horizontally. The density of alizarin uptake is indicated by the intensity of stippling. For abbreviations, see p. 216.

and intensity of alizarin uptake, the whole region is poorly calcified, and much remains cartilaginous.

The expansive, shield-shaped **lateral ethmoids** (Text-figs. 2 and 3) are probably the most heavily ossified elements, but even here the ventral, wing-like projection on each side is mostly cartilage, as is a large part of the lateral margin of each shield. The lateral ethmoids do not meet in the midline but are separated by a median ethmoid bloc which, in this region, is cartilaginous. There is a deep excavation for the olfactory nerve in the inner margin of each lateral ethmoid.

The **median ethmoid** (Text-fig. 2) is shaped like a broad-based and somewhat waisted pyramid. Anteriorly it is penetrated by a large cardiform foramen which is occluded by the underlying *planum ethmoidale*. This broad, thin sheet of cartilage forms a floor to the nasal capsules, and unites the ventral face of the lateral ethmoids with the median ethmoid bloc. Part of this bloc (especially in the midline) stains deeply and should presumably be identified as the mesethmoid (*sensu* Weitzman, 1967). Dorsally, this ossified region has a small area of contact with the antero-medial part of each lateral ethmoid. The anteromedial face of the palatine barely touches the lateral border of the median ethmoid bloc, which it overlies slightly. At the anterior angle of the bloc, there is a poorly defined facet with which the tip of the maxillary head is in articulation.

The toothless **vomer** (Text-fig. 3) is a very thin sheet of bone, almost circular in outline, and lying well-back from the anterior margin of the ethmoid bloc; thus it is only visible from the ventral side. Its anterior margin barely overlaps the posterior margin of the mesethmoid; posteriorly it overlaps the anterior tip of the parasphenoid.

The **nasals** (Text-figs. 3 and 5) are hook-shaped, gutter-like bones posteriorly contiguous in the midline, but widely separated anteriorly so as to form a U-shaped structure lying above the dorsal skull roof. At their medial point of contact each nasal is weakly attached to the underlying frontal near its anterior margin.

The posterior wall of the nasal, near its point of maximum curvature, is continued posterolaterally as a narrow, curved lamina. The lamina runs backwards at an angle of about 45° to the nasal, curving somewhat laterally to meet the anterior margin of the main frontal bridge (see below). After contacting the bridge and giving off a broad tongue of bone which overlaps it, the lamina curves along the anterior margin of the bridge. In this way the lamina almost completely occludes the anterior opening of the supraorbital laterosensory canal; however, a small open area remains laterally. The broad tongue extends across the width of the bridge, but is completely free from the underlying bone. Likewise, the entire ventral margin of the lamina is free from the underlying frontal. In an alizarin specimen the lamina is readily moveable and spring-like, always returning to its position against the anterior edge of the frontal bridge.

Orbital region. The **frontals** are large bones of rather complex form (see Text-figs. 3, 4, 5, 6 and 7). Above most of the orbit each frontal forms a flat shelf, but medial to this the bone is slightly arched towards the midline. The lateral margin of the supraorbital ledge carries a single row of stout odontodes anteriorly, but a double row posteriorly.

Behind the orbit, and extending ventrally to about the level of the eye's centre, the frontal forms an extensive temporal shield covering a large part of the anterior otic region. This temporal shield is divided horizontally by a deep but narrow indentation extending inwards from the posterior margin (Text-figs. 5 and 6). The upper flange so formed lies in a more superficial plane than the lower one, and overlaps it somewhat. The flanges together delimit the greater part of the temporal foramen; posteriorly, the foramen is without a definite superficial bony margin because the posteroventral tip of the parietal is directed away from this region.

The upper temporal flange carries a fairly dense patch of short and stout odontodes on its lateral face. This area of the frontal was mis-identified as the parietal in Clausen's original description of the species (see Greenwood, 1965).
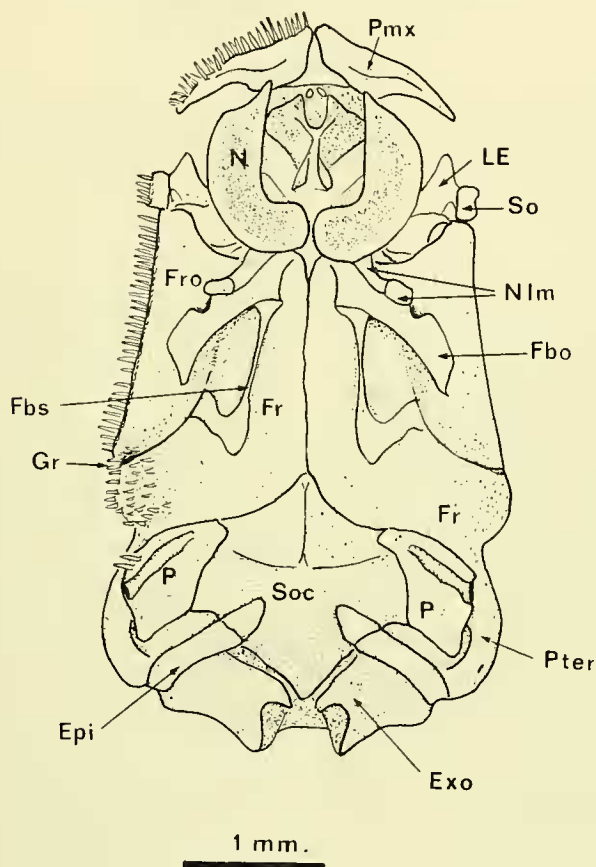

1 mm.

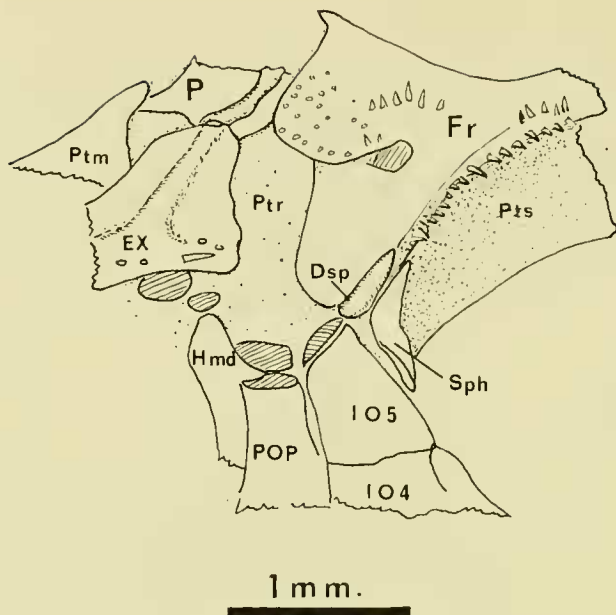FIG. 3. Neurocranium, dorsal view. Drawn from a different specimen than that used for Figs. 6 and 9.

FIG. 4.   Temporal region of skull to show dermosphenotic (Dsp) and openings to
recessus lateralis.   IO 4 and IO 5 : fourth and fifth infraorbital bones.

The lower temporal flange (together with the base of the upper flange) is continuous laterally with the ventrally curved postorbital extension of the supraorbital frontal ledge.   However, the transition is abrupt and gives rise to a deep but narrow, furrow-like groove, the base of which is slightly expanded.   This furrow follows the posterior outline of the orbit, and serves to link (*via* the short tubular dermosphenotic) the supraorbital lateral-line channel with the infraorbital canal and the *recessus lateralis* (see Text-fig. 5 and below).

At its upper end the furrow is bridged by a narrow strip of bone; thereafter it continues anteriorly in the slight groove formed in the angle between the supraorbital ledge and the curved medial part of the frontal.

The supraorbital lateral-line (including its temporal branch) is not enclosed in a bony tube.   Instead, the neuromasts lie superficially on the frontal and are contained in a cavernous space formed below two bony bridges over which the skin is stretched. One bridge, a broad, flat arch of bone spans obliquely across the supraorbital area from about the midpoint of the shelf to near the anterior margin of the arched medial part of the frontal (Text-figs. 3 and 5).   The second bridge is aligned parasagittally. It is an extremely narrow length of bone arising from a fairly broad base situated posteriorly near the opening of the nerve tube for the temporal neuromast.
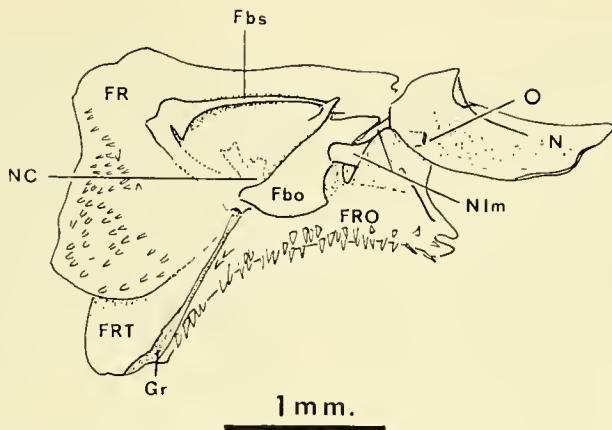
Fig. 5. Right frontal and nasal seen somewhat obliquely from above, to show supra-
orbital laterosensory region bridges (Fbs and Fbo), the nasal lamina (Nlm) and the
groove (Gr) leading from the dermosphenotic to the supraorbital laterosensory
chamber.

Anteriorly, this bridge ends near the medial end of the transverse one (Text-figs 3
and 5).

Further support for the skin roof of the supraorbital cavern is provided anteriorly
by the process derived from each nasal (see above, p. 220).   Besides providing sup-
port for the roof, these laminae serve as a lateral wall for the anterior part of the
cavern, and in this way connect the supraorbital and nasal laterosensory canals.
Further connection between these parts of the system is provided by a short bony
tube opening anteriorly into the floor of the nasal, and posteriorly into the groove
formed between the supraorbital and medial parts of the frontal.

On the ventral face of each frontal there is a narrow but prominent ridge following
the course of the postorbital groove for the lateral-line (see above).   The ridge is
directed somewhat medially.   Along most of its length it contacts the pterosphenoid,
while ventrally it articulates with the sphenotic.

Nerves supplying the posterior frontal neuromasts are carried in bony tubes on
the ventral face of the bone.   Two short tubes open close together into the posterior
part of the supraorbital groove; a third, much longer tube runs back to the temporal
region.   The latter canal opens at the posterior base of the parasagittal bridge.   Its
origin, on the ventral face of the frontal, lies behind the ridge described above, where-
as the two supraorbital tubes originate in front of the ridge.

Nerves supplying the anterior frontal neuromasts of the supraorbital line are not
enclosed in tubes, but gain access to the cavern through two foramina lying in the
anterior parts of the supraorbital groove.

The frontals contact one another along a barely sinuous median suture.   Their
anterior tips diverge slightly and each is intimately articulated with the dorsal margin

of a lateral ethmoid (Text-fig. 3). The median ethmoid cartilage barely touches the two frontals in the midline.

There is a single, small cuboid and densely " toothed " **supraorbital** bone on each side. Medially the supraorbital is attached to the lateral ethmoid, and posteriorly it articulates with the frontal. Clausen (1959) apparently interpreted the entire odontode-bearing margin of the frontal as a supraorbital bone (see his figure 1). Since there is no indication of fusion between the supraorbital ledge and the main body of the frontal, and because the element here identified as a supraorbital bone is readily separated from the frontal, I would dispute Clausen's identification.

The large unpaired **orbitosphenoid** (Text-figs. 6 and 9) is broadly U-shaped in cross-section, with a distinct median keel, low posteriorly but greatly expanded and ventrally produced anteriorly. Neither the main body of the bone nor its anteriorly directed keel contacts the ethmoid region.
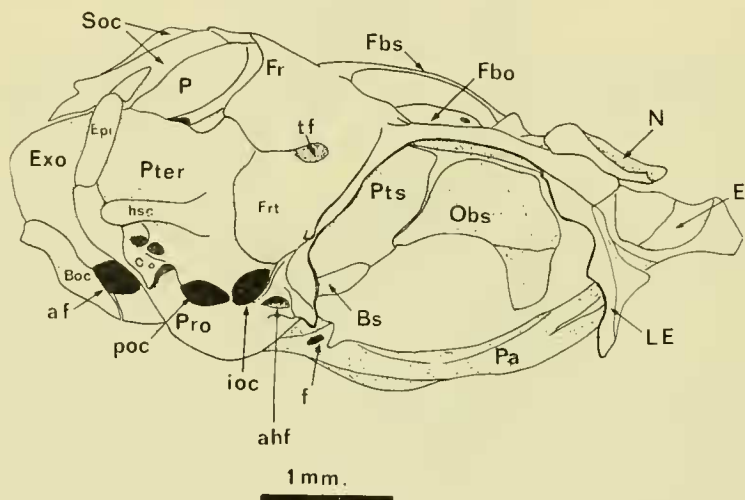

FIG. 6. Neurocranium in lateral view.

The paired **pterosphenoids** (Text-figs. 6 and 9) are in contact with the posterior margin of the orbitosphenoid anteriorly, with the frontals dorsally, and with the prootics and basisphenoid posteriorly and posterolaterally. At no point are the two pterosphenoids in contact with each other. Each is a large, broadly concave bone almost square in outline. Near the posterolateral angle is a notch which contributes to the medial margin of the large foramen opening into the *pars jugularis*. Posterodorsally the bone is pierced by a foramen for the trochlear nerve (IV).

Articulating with the ventromedial margin of each pterosphenoid is the unpaired, hexagonal and concavo-convex **basisphenoid**, its convex face directed anteroventrally. No ventral limb is present. The ventrolateral margins of the basisphenoid

articulate with a ledge on the face of each prootic; except for these points, the ventral margin has no other contact with the prootics. At these points of contact the basisphenoid is notched by a foramen for the oculomotor nerve (III), and there is a deep infundibular notch at about the middle of its ventral margin. The dorsal margin, in conjunction with the medial margin of each pterosphenoid, delimits a large foramen for the optic nerve (II).

Each of the paired **autosphenotics** is a short, stout and near conical bone, intimately connected dorsally with the descending postorbital wing of the frontal. Medially, the autosphenotic articulates with the pterosphenoid. The ventral face of the autosphenotic is deeply recessed and forms part of the articular facet for the anterior hyomandibular head. Its posterior face abuts against the pterotic to form the anterior wall of the *recessus lateralis*. Medially, the autosphenotic contributes to the margin of the anterior foramen of the *pars jugularis*.
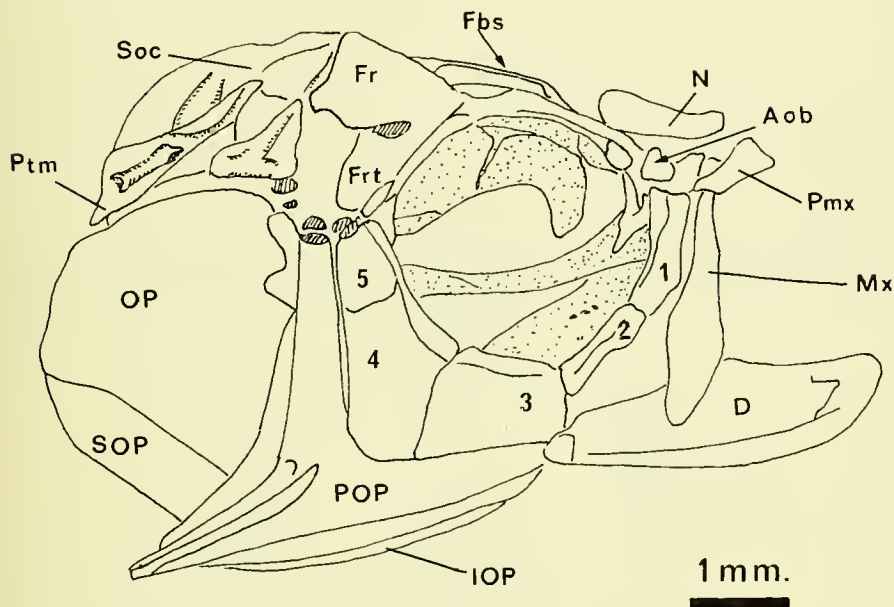

Fig. 7.   Syncranium; odontodes not shown.

Excluding the antorbital, there are six bones in the **infraorbital series** (Text-fig. 7). The small antorbital is a thin, poorly ossified triangular bone. It is free from the supraorbital above and is broadly connected below with the elongate and rather slender *lachrymal*. The infraorbital lateral-line canal is carried in a tube on the anterior half of the lachrymal, but beneath a flange from its upper margin on the posterior half. *Infraorbital 2* is also elongate and slender, but with a distinct notch at about the middle of its ventral margin; the lateral-line lies below a flange from

the upper border. *Infraorbital 3* is a deeper bone; the flange housing the sensory canal lies a little below its upper margin. Anteriorly, the flange appears to be formed entirely from odontodes, but posteriorly these are less dense and clearly arise from a shelf of bone. *Infraorbital 4* is the largest element in the series; as on the third infraorbital, the flange arises a little below the upper margin. *Infraorbital 5* is reduced to the flange, albeit a deep flange. In outline the bone is a truncated cone, U-shaped in section with the opening directed posteriorly.

The *dermosphenotic* (infraorbital 6) is the smallest element of the series and is reduced to a simple, slightly curved tube closely applied to the posterior face of the supraorbital flange of the frontal (Text-figs. 3–5). Dorsally it opens into the furrow formed between this part of the frontal and the lower temporal flange of that bone (see above, p. 222). Ventrally, its opening is directed towards the infraorbital foramen of the *recessus lateralis*, whose anterior border the dermosphenotic just contacts. The dermosphenotic is discussed further on p. 263.

Excepting the antorbital and dermosphenotic, all elements of the infraorbital series carry odontodes. On the lachrymal and on infraorbital 2 the odontodes are virtually confined to single rows bordering the upper and lower margins, and the upper margin of the bones respectively. Infraorbitals 3 and 4, however, are almost completely covered; only a narrow area above and below the lateral flange is naked. The anterior half of infraorbital 5 is naked, but the remainder has a fairly dense covering of odontodes.

The toothless **parasphenoid** (Text-figs. 2, 8 and 9) is so short that it barely extends beyond the confines of the orbit. In lateral view the parasphenoid is curved, with the anterior three-quarters sharply inclined. This ascending part has, at first, an inverted V cross-section but it broadens anteriorly into an inverted U. Just
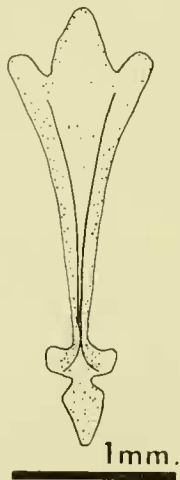

Fig. 8.   Parasphenoid (dorsal view), anterior end upwards.

behind its junction with the ethmoid, the parasphenoid flattens and divides into a broad, spatulate median region and two narrow, divergent lateral arms. The central part contacts both the vomer and the median ethmoid bloc, while the side arms articulate with the lateral ethmoids alone.

The posterior quarter of the parasphenoid is a narrow, compressed strut which slopes gently upwards towards the prootics. Before contacting the latter, it is produced into two short ascending arms which articulate with the anterior face of each prootic. There is a well-defined foramen for the internal carotid artery situated posterior to the base of each arm. The anterior face of each arm is deeply notched for the passage of the efferent pseudobranchial artery.

Except for a short medial tongue, the parasphenoid does not extend any further
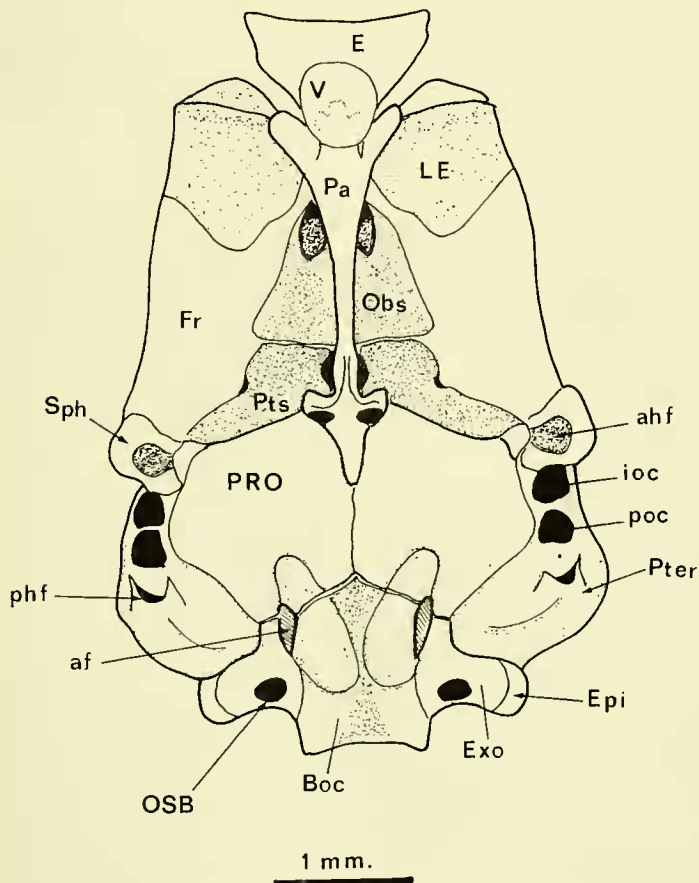

FIG. 9. Neurocranium, ventral view.

posteriorly than the anterior face of the prootics, a most unusual feature (see page 265). Since the prootics meet ventro-medially behind the posterior tip of the parasphenoid, the **myodome** is a very small affair. It is floored by the parasphenoid, has its lateral walls formed by the prootics and, except anteriorly where the basisphenoid arches over the interprootic gap, is without a bony roof. There is no obvious posterior opening to the myodome; but, the posterior tip of the parasphenoid stands slightly away from the ventral face of the prootics to leave a minute aperture.

Otic and occipital regions. (Text-figs. 9–15). The otic region has a decidedly inflated appearance due to the presence of especially large bullae surrounding the two paired intracranial swimbladder vesicles. The bullae are associated with the prootic and pterotic bones, which in consequence are the largest elements in the otico-occipital region of the skull.

When compared with the bullae of clupeoid fishes, those of *Denticeps* appear to be relatively much larger, and to have exerted a far greater influence in moulding the contours of the skull. To give some indication of relative bulla size, a comparison was made between a 6·5 mm. long neurocranium of *Denticeps* and a 40·0 mm. long
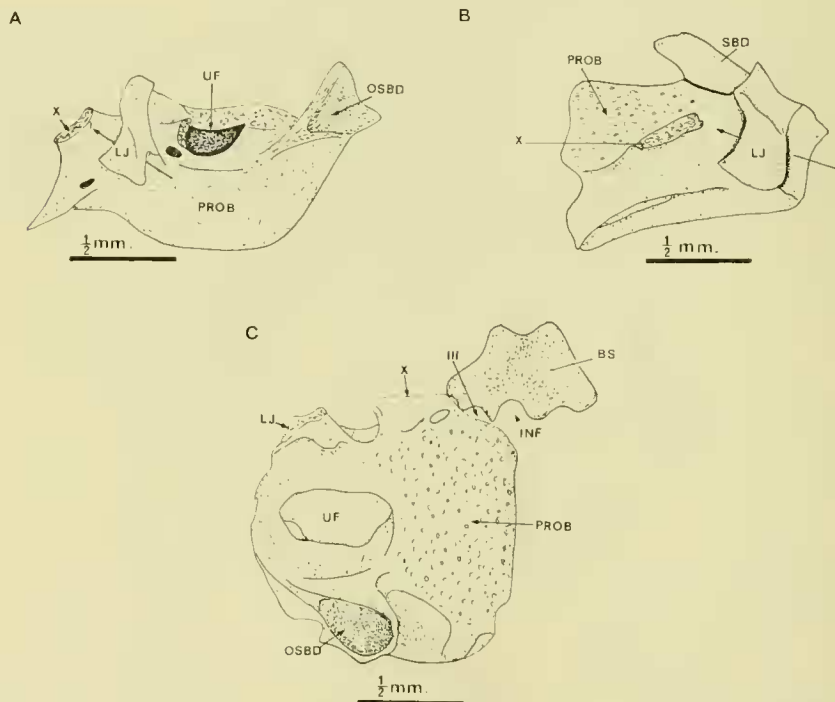

Fig. 10.   Prootic (left) and its bulla.   (A) Lateral view.   (B) Anterior view.   (C) Dorsal view (with basisphenoid, BS.).   The arrow indicates the *pars jugularis*.

neurocranium of *Clupea harengus*. The results are tabulated below; all measure-
ments are in millimetres, and represent maxima for the character:

	Prootic bulla		Pterotic bulla	
	Denticeps	*Clupea*	*Denticeps*	*Clupea*
Length	1·8	3·0	2·0	3·0
Depth	1·0	3·0	2·0	3·0
Breadth	1·0	3·5	1·0	3·0

Since it is difficult to differentiate between the **prootic** (Text-figs. 6, 9 and 10)
and its associated bulla, the combined structure will be described.

The bulla is in the form of a somewhat compressed and truncate ovoid with the
long axis transversely aligned, and the truncated face directed medially. As far as
I can determine, the prootic proper sheathes the anterior, ventral and a greater part
of the medial aspects of the bulla.

On the anterior face are two ridges. The upper and shorter ridge provides articu-
lar surfaces for the basisphenoid and pterosphenoid bones. It is pierced near its
medial margin by a tunnel-like foramen. The lower ridge is longer and lies near the
ventral edge of the bone. Its medial margin is drawn out into an anteriorly directed
spur which contacts the short ascending limb of the parasphenoid. The ridge runs
laterally and somewhat dorsally to unite with the base of the broad lateral com-
missure of the *pars jugularis*. The commissure slopes upwards and forwards to reach
the upper margin of the prootic. It is so orientated that its face is directed almost
anteriorly. From the upper, posterior corner of the commissure there is a narrow
ledge of bone which follows the outline of the upper lateral margin of the prootic
to its termination. This ledge provides an articular surface for the pterotic, and
also serves as the floor for the *recessus lateralis*.

The ventral face of the prootic is smooth except for a short spatulate depression
extending forwards from about the middle of its posterior margin; this depression
floors the anterior part of the saccular cavity.

The prootic bulla has two openings. One is situated dorsally and opens at the
base of the utricular recess. The other, and smaller, opening is funnel-shaped and
lies at the posterolateral edge of the bulla. It is the entrance for the swimbladder
diverticulum, and is continuous with a similar shaped dilatation of the exoccipital
base. (The swimbladder diverticulum enters the skull through the exoccipital.)
Below and medial to this funnel, the bulla is invaginated for almost its entire width
and for about a third of its length. The concavity so formed is the anterior part of
the saccular recess.

The prootics of each side are in contact medially over most of their apposed faces.
Anteriorly they curve slightly away from one another to form a shallow cleft which
serves as the posterior myodome (see above, p. 228).

Since the *pars jugularis* of the *trigemino-facialis* chamber lies almost entirely in the
prootic it can be described here. It is of a simple type with a single *trigemino-
facialis* foramen opening into its anterior part. Most of the foramen margin is

derived from the prootic, but it is completed dorsally by the pterosphenoid (see p. 224); the lateral commissure is described above.   The orbital artery does not have a separate foramen but passes into the *pars jugularis* through its posterior opening (as in clupeoids).   However, unlike the condition found in clupeoids, there is no distinct foramen for the hyomandibular branch of VII.   This branch shares the posterior opening with the head vein and the orbital artery.   In this respect the *pars jugularis* of *Denticeps clupeoides* resembles that of perciform fishes (see Patterson, 1964).

The *pars ganglionaris* of the chamber is a narrow shelf projecting from the inner prootic face immediately medial to the *pars jugularis*.

Like the prootic, the **pterotic** is intimately associated with its bulla, and the two bones cannot be separated readily (Text-figs. 6 and 11).   The pterotic, however, sheathes only the lateral and posterolateral aspects of the bulla.   In adult animals it is impossible to distinguish between dermal and endochondral pterotic elements since only a single sheet of bone is present.   The situation is further complicated when, as in this case, a *recessus lateralis* is developed and in consequence the laterosensory canal lies medial to the bone and not superficially on any part of it.
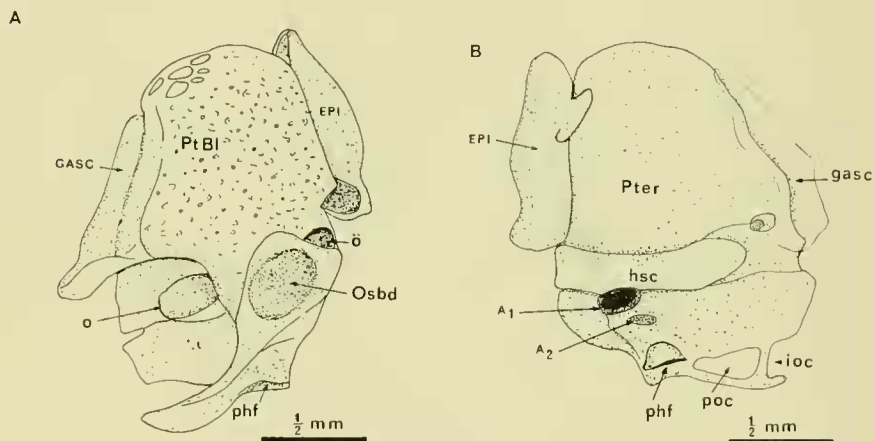

FIG. 11.   Pterotic (right), pterotic bulla, and the epiotic.   (A) Median view.   (B) Lateral view.

The pterotic is approximately ovoid in lateral outline, the narrower pole directed upwards; slightly below the equator, the bone bulges a little around the horizontal semicircular canal.   Over its ventral third the bone is slightly bowed in the vertical plane, with the concavity facing inwards.   The anteroventral angle is deeply notched, the notch being separated by a narrow vertical pillar from a large foramen immediately behind it.   In an entire neurocranium the notch is closed anteriorly by the sphenotic, and forms the first of four foramina opening into the *recessus lateralis*. Through it the infraorbital and supraorbital laterosensory canals open into the

recessus; the succeeding foramen receives the opening of the preopercular sensory canal (Text-fig. 11B).

Just behind the preopercular foramen there is a projecting, cup-like eminence, the articular facet for the posterior hyomandibular head. Above this facet lie the third and fourth openings into the *recessus*. Of these foramina, the upper (and larger) is surrounded by a prominent margin so that it projects well beyond the general level of the bone. This opening receives the laterosensory canal from the extrascapular bone. The lower and smaller foramen has no obvious connection with a superficial canal. By analogy with the typical clupeoid condition (see Wohlfahrt, 1936, 1937) it should connect with an extratemporal canal, but I was unable to verify this point.

The **pterotic bulla** has a slightly greater volume than its prootic counterpart. It is best seen from the medial aspect. It is a compressed ovoid with a broad posteroventral stalk, opening medially, through which the duct of the swimbladder vesicle passes. The stalk is delimited from the main body by two indentations; one accommodates the utricular sac, the other the horizontal semicircular canal. It is separated from the pterotic laterally by the chamber of the *recessus lateralis*. A short but broad horizontal wing arises from the anterior face of the bulla immediately above the horizontal semicircular canal groove. This wing is continued laterally and dorsally to a point near the dorsal pole of the capsule. Its outer face is deeply concave and surrounds the anterior semicircular canal medially. The anterodorsal surface of the bulla is finely fenestrated, and is crossed by the anterior semicircular canal.

The **intercalar** (opisthotic) is absent.

The **recessus lateralis,** mentioned in connection with both the prootic and pterotic bones, is a peculiar feature of clupeomorph fishes (see Greenwood *et al.*, 1966). Essentially it is a chamber, developed in the otic region, into which all the major cephalic laterosensory canals open (see Wohlfahrt, 1936, for a detailed anatomical description). The lateral wall is provided by the pterotic and, in *Denticeps*, it has four openings. The first is shared by both the supra- and infraorbital laterosensory canals, the former being led in through the dermosphenotic (see Text-fig. 4). In this respect the *recessus* of *Denticeps* differs from all other clupeomorph fishes I have examined or which have been described. A typical clupeoid *recessus* has a separate opening (from the medial side) for the supraorbital canal, and often a small part of the frontal bone contributing to its roof. (A possible exception to this generalization is found in the engraulid genus *Coilia*, where the *recessus* is invaded by the prootic bulla and consequently is considerably modified; nevertheless, it is certainly not of the *Denticeps* type.)

In *Denticeps*, as in the clupeoids, the floor of the *recessus* cavity is provided by the prootic, and there is no bony medial wall, the cavity being separated from the perilymph cavity by a membrane. Its roof is entirely of pterotic origin (other clupeoids have a small frontal contribution), but part of the anterior wall is provided by the autosphenotic.

The elongate, semitubular and slightly arched **epiotic** (Text-fig. 11) is firmly attached to the posterodorsal surface of the pterotic and the underlying portion of

the bulla. It is little more than a bony cover intimately applied to the semicircular canal. On its anterior face, however, there is a narrow tab which is closely applied to the pterotic (Text-fig. 11B).

No trace of a preepiotic fossa could be found; possibly it has been obliterated by the expansion of the pterotic bulla.

The otic region is floored by the paired prootics anteriorly, and the median basi-occipital posteriorly. As will be recalled (p. 226) the parasphenoid does not extend much further posteriorly than the forward margin of the prootics (Text-fig. 9). The **basioccipital** (Text-fig. 14) is about as long as the prootics, and almost rect-angular in dorsal outline. Its floor is deeply recessed on either side of a broad-based median ridge running the entire length of the bone. Arising from the ridge are two wing-like flanges which curve gently outwards to provide part of the median wall and roof of the saccular recess lying in the basioccipital floor.

The anterior face of the basioccipital is firmly articulated with the prootics, and the posterior face contributes to the tripartite occipital condyle for the first vertebra (see below).

An **auditory fenestra** (bounded by the prootic, exoccipital and basioccipital) is present on each side of the skull posterior to the prootics and below the ventral edge of the pterotics (Text-figs. 6 and 9). At least in an alizarin preparation, part of the saccular otolith can be seen through the fenestra.

The posterior face of the skull is formed partly from the paired exoccipitals and partly by the supraoccipital. Each **exoccipital** (Text-fig. 12) is a vertically elon-gate, relatively narrow bone with a bulbous basal region in which is lodged the pos-terior wall of the saccular recess and part of the posterior semicircular canal. Below and posterior to the bulge of the semicircular canal is a single large foramen for the glossopharyngeal (IX) and vagus (X) nerves. Also opening into this region is a
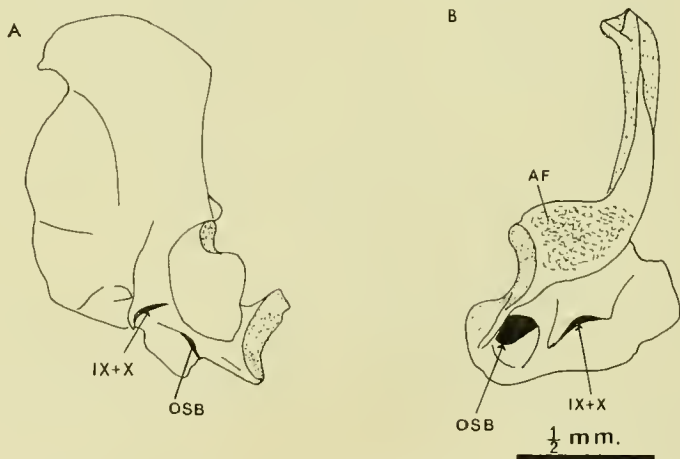

FIG. 12. Exoccipital (right). (A) Lateral aspect. (B) Posterior aspect.

funnel-shaped tube through which the anterior prolongation of the swimbladder enters the neurocranium. This passage connects with its mirror image in the prootic, and with the ventral opening of the pterotic bulla.

The anterior margin of the exoccipital is firmly articulated with the pterotic, the basal part with the basioccipital behind the auditory fenestra, while the antero-dorsal tip contacts the supraoccipital above. The dorsoposterior tips of the exoccipitals do not quite meet above the *foramen magnum* but are apparently connected by a small wedge of cartilage.

Internal to the *foramen magnum*, a short median shelf from the inner face of each exoccipital contacts the corresponding wing of the median basioccipital lamina, thus roofing the posterior part of the saccular recess.

On the posterior face of the exoccipital bone there is a rough-surfaced facet directed medially and ventrally (Text-fig. 13). The facets on each exoccipital, together with the median basioccipital facet, form a tripartite condyle for the first vertebra. The rough anterior face of this vertebra is bevelled to fit closely with the facet, and can only be prised from it with some difficulty.
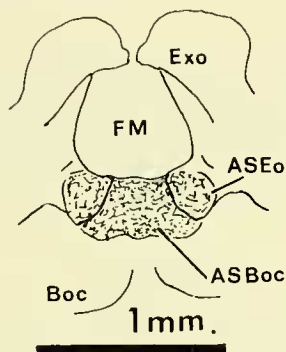

FIG. 13.   Condylar surfaces for the first vertebra.

A condyle of this type is not present in any of the clupeoids I have examined. There is a certain resemblance, however, to the condition found in the osteoglossid *Heterotis niloticus*, the hiodontid *Hiodon alosoides*, and in the elopoid *Megalops cyprinoides*. In the latter, the union of vertebra and skull is more complete than in *Denticeps*, and the centrum of the first vertebra is short. Furthermore, the neural arch associated with this centrum is lost in *Megalops* but is present in *Denticeps*.

Ridewood (1904), commenting on the occipital condyle in various lower teleosts (including six clupeoid genera) concluded that in all, the remnants of a half-centrum was incorporated in the condyle. Thus, *Denticeps* would seem to preserve an early stage in the evolution of a condyle type found in most lower teleosts. The condition found in *Heterotis* (where a complete neural arch, pleural rib and epicentral bones are associated with the centrum), however, appears to be at an even more primitive stage.
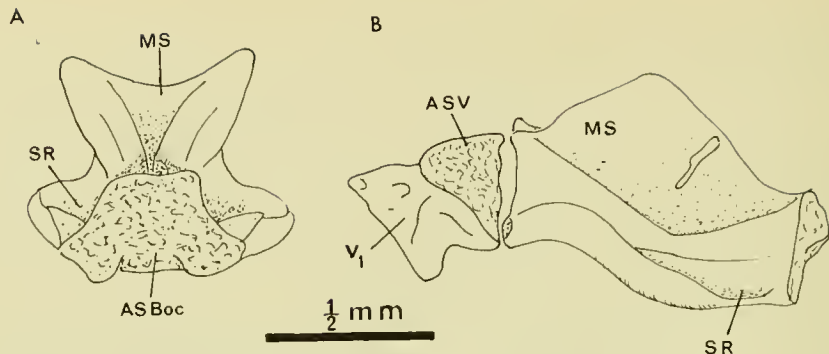
FIG. 14.   Basioccipital and first vertebra.   (A) Posterior view of basioccipital.   (B) Lateral
view (right) of basioccipital and first vertebra.

The **supraoccipital** (Text-figs. 3 and 15) is a large and expansive bone bent transversely about its midpoint through almost 45°.   The dorsal (i.e. horizontal) part is largely covered by the posterior part of the frontals, and laterally by the parietal tips.   A few weak odontodes occur on the exposed part of the horizontal surface.   At the point of flexure there is a transverse groove interrupted in the midline by a lateral expansion of the low sagittal crest which extends slightly forward from the posterior (i.e. sloping) part of the bone.   The dorsomedial tip of each
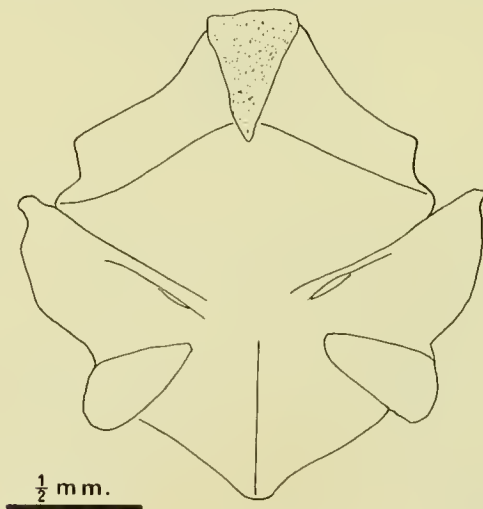

FIG. 15.   Supraoccipital (dorsal aspect), the anteroposterior axis aligned horizontally.

parietal fits into the respective lateral limits of the groove. Thus, the groove continues the course of the parietal laterosensory canal.

The sloping posterior face of the supraoccipital has a low, broad-based sagittal ridge; laterally it is marked by well-defined protuberances indicating the position of the uppermost portion of the posterior semicircular canals.

Anteriorly and anterolaterally the otic region is roofed by the frontals whose temporal flanges cover the anterolateral parts of the pterotics. The latter bones are also partly roofed by the parietals.

Each **parietal** (Text-figs. 3 and 6) is a flat, scale-like bone approximately rectangular in outline but with the anteromedian angle somewhat produced. A laterosensory canal crosses the parietal slightly anterior to the middle of its lateral margin. This canal opens into the transverse groove of the supraoccipital (see above). Except for a narrow area, all that part of the parietal lying in front of the tube is overlain by the frontal. The remainder of the parietal overlies the dorsolateral surface of the pterotic bulla, to which it is firmly joined. A single line of odontodes runs along the laterosensory tube, and there is a small patch on the narrow exposed area between the frontal margin and the tube.

In his original description of *Denticeps clupeoides*, Clausen (1959) misidentified the upper temporal flange of the frontal as a parietal. Thus he was led to think that the parietals meet in the midline. The true parietals, however, do not meet since they are separated by the broad sagittal ridge of the supraoccipitals. Also as a result of this misidentification, Clausen described the temporal foramen (his " postemporal foramen ") as being " roofed over mainly by the parietal ". It is in fact contained entirely within the frontal (but with an open posterior margin, see page 221).

Much of the dorsolateral pterotic face is covered by the **extrascapular** (Text-fig. 4) which is loosely joined along its anterior margin to that bone. The posterior margin stands slightly away from the pterotic, and is articulated with the posttemporal (see below). The thin plate-like extrascapulars are broadly triangular in outline, the apex pointing posteriorly. The extrascapular laterosensory canal is triradiate; the upper arm passes to the parietal canal, while the much shorter lower arm passes to the upper of the posterior two *recessus* foramina in the pterotic. The only odontodes present lie in a single line partly along the lower laterosensory tube and partly on the median tube.

Oromandibular region. The **premaxillae** (Text-figs. 3 and 7) are short bones (about half the length of the maxillae), with a fairly marked curvature in the horizontal plane, and moveably apposed to one another in the midline. As seen through the dense pile of odontodes covering the lateral surface of the premaxilla, the bone appears loosely cancellous. The odontodes are reduced to a single row of relatively spaced teeth on the ventral margin.

Along the posterior half of the medial face and near the ventral margin there is a narrow shelf of bone. Anteriorly this shelf widens considerably, and its inner margin curls inwards to form a broad groove. Part of the maxillary head slips under the posterior shelf and the inner wall of the anterior groove lies on the ethmoid, over which it has a restricted area of sliding movement.
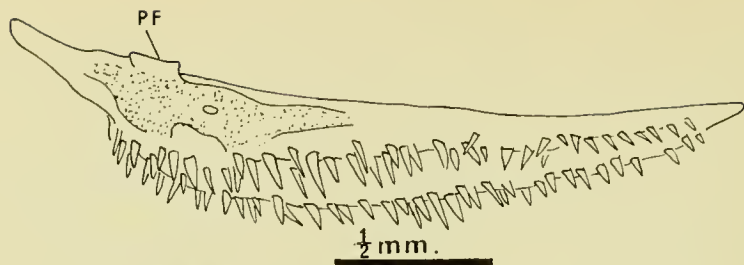
FIG. 16.   Maxilla (left) seen somewhat obliquely from above.

Each **maxilla** (Text-fig. 16) is an elongate, flattened, lanceolate bone abruptly narrowing anteriorly to form a distinct head, cylindrical basally but flattened distally.   At the point where the head joins the blade there is a dorsally directed elongate facet for articulation with a similar facet on the palatine.   The dorsal margin of the maxillary blade is thickened over its anterior half; a shallow, barely discernible groove runs almost the complete length of the blade.

The maxilla is less densely " toothed " than the premaxilla.   A double row of odontodes extends along the upper lateral margin of the blade above the groove and is continued posteriorly beyond the groove almost to the tip of the bone.   Another double row runs along the lateral face of the lower maxillary margin, and there is a single row along the margin itself (that is, in the usual position of the maxillary teeth).   The area between the upper and lateral odontode rows is bare, and noticeably so.

The maxilla articulates with the palatine through a distinct flat facet.   It has a second articulation (through the anterior tip of its head) with the anterolateral corner of the ethmoid, but here no distinct facets are developed.   A third articulation point may be present between the maxillary head and the anterolateral face of the palatine.   All these joints are simple sliding surfaces and only in the case of the palato-maxillary articulation are definite facets developed on the apposed surfaces.   In preserved specimens very little upper jaw movement can be achieved by manipulation.

When the mouth is closed, only a small area near the maxillary head slips under an infraorbital bone, the rest of the maxilla lying ventral to the infraorbital series.

No supramaxillae are present.   Like Clausen (*op. cit.*), I can find no trace of a supramaxilla–maxilla suture.   But, the conspicuous longitudinal area free from odontodes is not readily explained, and should be carefully examined from the ontogenetic viewpoint if embryos become available.

Lower jaw (Text-figs. 7 and 17).   The **dentary** is a long, slender bone, somewhat thickened in the mental region, and with only a slight coronoid eminence.   The mandibular laterosensory canal runs along the ventral third of the dentary.   Over the posterior half of its course it is an open groove, but anteriorly it is enclosed in a tube.   The tube opens anteriorly into a short groove and is perforated along its length by at least four small openings.

Most of the lateral face of the dentary is without odontodes. There are, however, dense patches of elongate odontodes covering the anterior and posterior quarters of the lateral face. These two areas are connected by a linear patch (two rows deep posteriorly, becoming multilinear anteriorly) situated along the ventral margin of the lateral face. On the ventral face (which slopes medially at a gentle angle) odontodes occur in a single line on the tubular part of the laterosensory canal, and in several rows along the ventromedial margin.

An initially double but posteriorly single row of odontodes extends along what would normally be the alveolar surface of the dentary. It reaches posteriorly to beyond the hinder level of the posterior lateral odontode patch, thus extending along about the anterior third of the coronoid eminence. There is complete spatial continuity between the anterior lateral odontode patch and the odontodes forming the mandibular " tooth-row ", and no difference in the external appearance of the odontodes and the teeth.
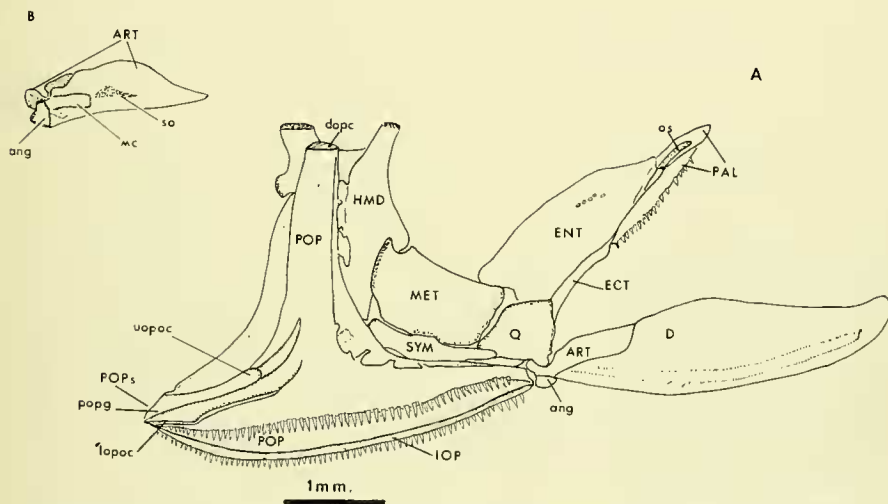

FIG. 17.   (A) Lower jaw, palatoquadrate arch, preoperculum and hyomandibula (right), in lateral view.   (B) Articular (left) in medial view.   The bases of the entopterygoid teeth are shown as circles.

The **articular** (angular of authors) is an elongate, rather shallow bone that penetrates deeply into a narrow longitudinal recess of the dentary (Text-fig. 17). Posteriorly it is thickened, the dorsal surface provided with a deep, hook-like notch for articulation with the quadrate; the posteroventral margin is excavated to receive the retroarticular. Medially there is a well-developed and ossified portion of Meckel's cartilage (the articular of authors), preceded by a slender, spicule-like sesamoid articular. On the lateral face there is a sensory canal crossing obliquely downwards

below a dense patch of elongate odontodes; it links the preopercular and dentary laterosensory canals.

The **retroarticular** is a fairly large bone, with about its ventral half exposed, the remainder lying medial to the articular. No odontodes are developed on this bone.

Palatoquadrate arch (Text-fig. 17). The **palatine**, in dorsal view, has the appearance of an arrow head. The slender posterior arm is capped anteriorly by a broad flat head, bearing on its lateral face a well-defined articular facet for the maxilla. Although the anterior tip of the head touches the ethmoid (see above, p. 220), no facet is developed. An irregular double row of teeth runs along the entire ventral length of the palatine arm. The medial face of this arm is firmly united with the anterior half of the lateral face of the entopterygoid.

The **entopterygoid** (Text-figs. 17 and 33) itself is a thin, poorly ossified and gently curved sheet of bone with, at about its middle, a row of five tiny teeth. Anteriorly, the medial entopterygoid margin slightly overlaps the lateral part of the parasphenoid, but posteriorly it is quite free from that bone.

The **ectopterygoid** is a slender bone, slightly curved near its posterior end. For most of its length, the ectopterygoid is in firm contact with the posterior half of the lateral entopterygoid margin; its tip is firmly united with the palatine, and the curved posterior part lies in a corresponding indentation of the quadrate. The union between ectopterygoid and quadrate seems a very loose one.

Each **metapterygoid** (Text-fig. 17) is an expansive, well-ossified and nearly rectangular bone. Anteriorly, the metapterygoid has a firm but flexible junction with the posterior face of the quadrate. Posteriorly there is a deep, flap-like projection which slightly overlaps, and is firmly joined to the underlying part of the outer hyomandibular face.

The main body of the **quadrate** (Text-fig. 17) has the typical quadrant outline of this bone; its ventral margin is produced posteriorly into a narrow, handle-like projection underlying the metapterygoid and symplectic for some distance. There is a narrow but deep notch between this handle and the quadrate body into which the symplectic is inserted. At its anteroventral angle, the quadrate bears a simple condyle for articulation with the notch of the articular, and its anterodorsal angle is recessed to receive the curved posterior end of the ectopterygoid.

Opercular series (Text-figs. 17 and 18). The **preoperculum** has a very characteristic outline, and a decidedly inflated appearance resulting from the enlarged laterosensory canals which occupy most of the bone.

Its anterior outline has a typical crescentic curvature, but the posterior margin is drawn out into a substantial spine-like process. At first sight, the posterior spine appears to be double; however, the " division " is actually a narrow groove of poorly ossified bone.

Immediately above the groove are two openings to the laterosensory canal. The ventrally directed lower opening is a long slit. It is connected with the main canal by an elongate tube which runs parallel to a shallow groove leading away from the upper opening. The latter is semicircular and narrow; it is linked to the main canal by a short tube.
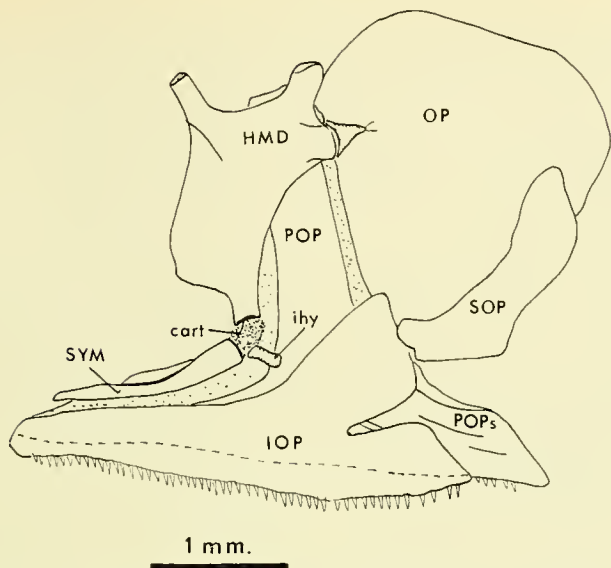
FIG. 18. Hyomandibular and opercular series (right) in medial view.

The main part of the laterosensory canal occupies most of the ascending limb of the preoperculum, and expands ventrally to fill almost the entire horizontal limb except for a small area anteriorly. The ventral wall of this canal is perforated by four extensive openings separated by narrow struts of bone. The ventral margin of the preoperculum is therefore, double. Its smooth inner margin projects further ventrally than the outer margin, which is fringed with odontodes (Text-fig. 17). Odontodes also border the margin of the upper laterosensory canal in the posterior spine, and occur irregularly over the entire exposed lateral face of the preoperculum.

The anterior preopercular angle is filled by the third and fourth infraorbital bones. The distal margins of these bones fit into a flange formed by the junction of the inflated, canal-bearing part of the preoperculum and a narrow ledge of bone which outlines the anterior margin. A similar narrow flange delimits the posterior preopercular margin.

The **interoperculum** (Text-figs. 17 and 18), although flimsy and poorly ossified, is an expansive bone (*pace* Clausen, 1959), whose outline and area is almost equal to that of the anterior and posterior horizontal part of the preoperculum, so that in lateral view little more than its toothed ventral margin protrudes. The odontodes fringing the interoperculum are arranged in a double row anteriorly but a single one along about the posterior half.

The **suboperculum** (Text-fig. 18) is also a flimsy bone, and is much narrower

and more linear in outline than the interoperculum. It underlies the entire ventral margin of the operculum which overlies its upper third. A few scattered odontodes occur over the exposed surface (apparently absent in the specimens examined by Clausen [*op. cit.*]). Clausen compared the suboperculum of *Denticeps* to that in osteoglossids, on the grounds that it is " partly hidden under operculum ". However, the bone is relatively larger and more exposed in *Denticeps* than in the osteoglossids; it is, 1 think, more readily comparable with the clupeoid condition.

The only outstanding characteristics of the **operculum** (Text-figs. 1 and 18) is its odontode distribution pattern. The odontodes are arranged in six or seven, somewhat curvilinear rows separated by distinct interspaces. Each row may be double in places, and none except the last row extends over the upper two-fifths of the operculum. Even the last row (which lies along the posterior margin of the operculum) does not extend beyond the dorsoposterior angle of the bone.

Odontode distribution is clearly influenced by the development of dermal laterosensory canals on the operculum (see p. 266, and Clausen, *op. cit.*); the rows are confined to the interspaces between the canals. The absence of odontodes dorsally is due to the contiguity of the dermal canals in that area.

Hyoid arch. The **hyomandibula** (Text-figs. 17 and 18) has a broad main body, whose distal end narrows abruptly into a short vertical limb distally tipped with cartilage. There are two prominent articular heads, the anterior somewhat narrower than the posterior one. A prominent perforated ridge runs across the lateral face from the base of the anterior head to the posterior margin of the bone; it ends near the tip of the narrow distal limb. The preoperculum fits into the posterior face of this ridge. A large oval foramen for the hyomandibular branch of the facial nerve penetrates the hyomandibula near its centre.

The anterior hyomandibular head articulates with a deep, conical socket formed mainly in the sphenotic, but also partly from the prootic. The posterior head fits into a horizontally aligned conical projection from the pterotic.

The short **interhyal** (Text-fig. 18) is barrel-shaped, and is attached to the cartilaginous area between the hyomandibula tip and the symplectic.

The **symplectic** (Text-fig. 18) is an elongate, slightly angled bone. Its anterior tip inserts deeply into the quadrate, and its entire posterior ventral surface is closely bound to the preoperculum. The posterodorsal surface is intimately associated with the ventral margin of the metapterygoid. Proximally, the symplectic articulates with the hyomandibula through an extensive synchondrosis.

The **epihyals** (Text-figs. 20 and 21) are fairly stout, shield-shaped bones each bearing laterally a single branchiostegal ray (see below). Union between the epihyal and the ceratohyal of its side is through a flexible syndesmotic joint.

Each **ceratohyal** (Text-figs. 20 and 21) is axe-shaped, the forward pointing " handle " expanded anteriorly to form a double articular surface, the smaller facet of which contacts the dorsal hypohyal, and the larger ventral surface contacts the ventral hypohyal. Four branchiostegal rays articulate laterally with the ventral margin of the expanded " axe-head " of the bone. This margin is slightly sinuous but the contours cannot be correlated with the position of individual branchiostegal rays.

Both the epi- and ceratohyals of each side are traversed by a tubular canal housing the hyal artery. The tube opens anteriorly on the dorsal aspect of the ceratohyal and posteriorly it opens on the lateral face of the epihyal.

The paired **dorsal hypohyals** (Text-figs. 22 and 23) are small, ovoid bodies closely applied to the posterior tip of the basihyal on its ventral surface. The ventroanterior tips of the dorsal hypohyals articulate with the underlying postero-dorsal tips of the ventral hypohyals through a very small point of contact. Posteriorly they approach closely the anterior tip of the first basibranchial but do not actually contact that bone.

The **ventral hypohyals** (Text-figs. 22 and 23) are much larger, pyramidal bones, also separated narrowly in the midline. They articulate with the dorsal hypohyals and more extensively, with the head of the ceratohyals.

The unpaired, median **basihyal** is a poorly ossified elongate bone (Text-fig. 22), hemicylindrical in section and somewhat broader anteriorly than posteriorly. It articulates with the dorsal hypohyals, and with the anterior tip of the first basi-branchial. Continuous with its cartilaginous anterior tip is a small hemispherical nubbin of cartilage (Dr. G. Nelson, who has examined the material, interprets this as a case of secondary segmentation of the basihyal, in his experience an unusual occurrence).

No teeth are present on any part of the hyal skeleton.

The **urohyal** is a poorly ossified, elongate and rather slender bone; except for a short distance anteriorly it has a double ventral margin, the bone being an inverted " V " in cross-section.

The **branchiostegal rays** (Text-figs. 19 and 20) have been mentioned briefly above. In all specimens examined by Dr. Clausen and me there are five pairs of rays. Of these, four articulate with the ceratohyal, and one with the epihyal. The branchiostegals show an anteroposteriorly progressive expansion, although the first ray has the broadest proximal articular surface. The third to fifth branchiostegals also show an increasingly marked indentation of the anterior face which, on the fourth and fifth rays, could be described as notched.
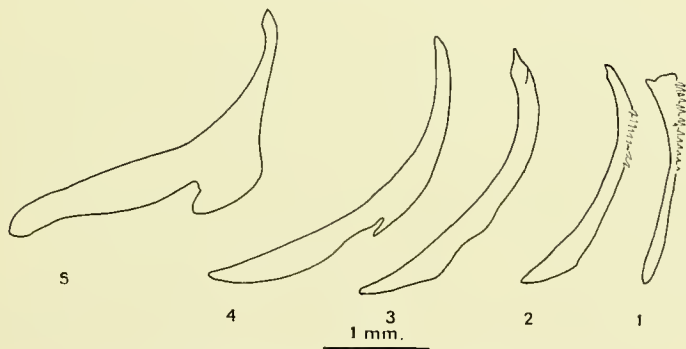

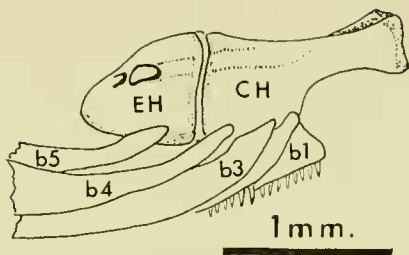Fig. 19. Branchiostegal rays (right) in lateral view.

FIG. 20.   Part of hyal arch (right), and branchiostegal rays *in situ*; lateral view.

Odontodes are present on the anterior margin of the first and second rays only (Clausen reports them present on the first ray only).

Branchial skeleton (Text-figs. 21 and 22).   An outstanding feature of the branchial skeleton in *Denticeps* (especially as compared to most clupeoids, all elopomorphs and all osteoglossoids) is the marked reduction in the number of dermal tooth-bearing plates associated with the gill-arches.   *Denticeps* also stands apart from all clupeoids in the relative proportions of the various arch elements (particularly the hypo- and ceratobranchials of arches I and II).   These and other characters will be discussed elsewhere (p. 269).

Each of the first four gill-arches has an **infrapharyngobranchial,** that of arch IV being very poorly ossified or even cartilaginous.

Infrapharyngobranchial I (I.P.H. I): is short, slender and cylindrical, and is directed anteromedially.

I.P.H. II.   is elongate, flattened-cylindrical in cross-section, slightly angled a little anterior to its midpoint, the dorsolateral face with a low swelling at the point of inflection; anterior tip parallel with that of I.P.H. I.

I.P.H. III: is about as long as I.P.H. II, but is flatter and has its posterior tip expanded and foot-like; its anterior tip is orientated sagittally.

I.P.H. IV: is small, roughly rectangular (narrowed anteriorly), and poorly ossified or cartilaginous.

The infrapharyngobranchials do not come together in the mid-line (as they do in most clupeoids, see Nelson, 1967) but are separated by a fairly wide gap.

Epibranchials (E.B.) are present on the first four arches.

E.B. I and E.B. II: are similar in shape (elongate rectangular), the second slightly smaller.

E.B. III: is noticeably more slender than the preceding epibranchials.   It bifurcates at about its midpoint; the dorsally directed posterior arm is slightly shorter and more slender than the medially directed anterior arm.

E.B. IV: has the posterior part triradiate and more heavily ossified than the anterior portion.   The arms of the triradiate part meet in a Y junction. The space between the short posterodorsally directed arm and the tail of the Y is filled by a thin sheet of bone so that the posterolateral part of the epibranchial is triangular in outline.
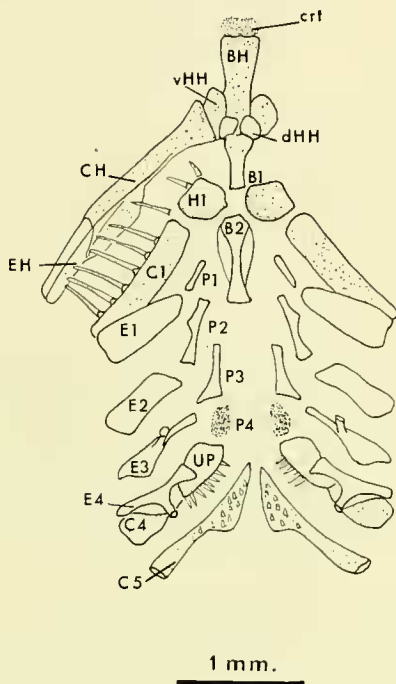

1 mm.

FIG. 21.   Branchial skeleton and left hyal arch, seen from above.   Gill rakers are shown only on the lower part of the first gill arch. crt : cartilage.

The **ceratobranchials** (C.B.) of gill-arches I to IV are similar, that is, elongate, rather flattened cylinders; the proximal (ventral) tips of ceratobranchials III and IV are slightly expanded.   The ceratobranchial of arch V is narrow but has on its posterior face, near the proximal end of the bone, a tooth-bearing expansion.

Hypobranchials (H.B.) are present in the first three gill-arches.

H.B. I: is short and square.

H.B. II: is also short, but is roughly diamond-shaped in outline, the bones of each side apparently linked by an ill-defined cartilaginous plate.

H.B. III: is a slender, roughly T-shaped bone, the crosspiece short and obliquely aligned to the longer shaft; from the medial tip of the cross-piece a ventrally directed bar forms, with its partner of the opposite side, an

aortic canal. The posterior tip of the main shaft is cartilaginous and contacts the cartilage plate between the bases of ceratobranchials IV and V.
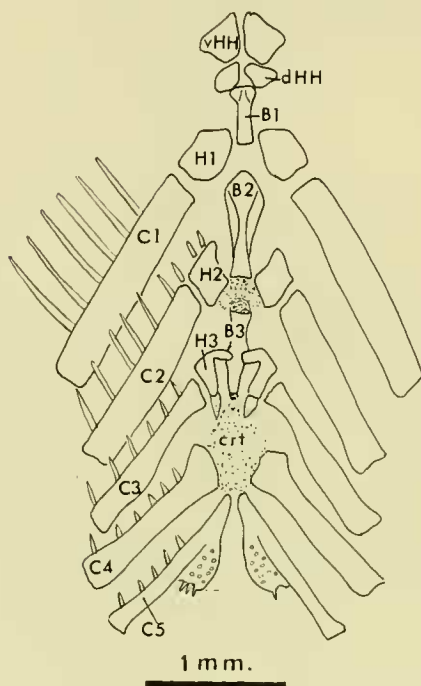

FIG. 22. Branchial skeleton and hypohyals, ventral view. crt : cartilage.

Ossified, median, unpaired **basibranchials** (B.B.) occur between the first three gill-arches only. At the base of arch IV there is a thin cartilaginous plate which, at least in part, represents an unossified fourth basibranchial.

The three ossified basibranchials are long, slender bones, each with an expanded anterior tip. Basibranchial II is the longest and broadest element of the series; viewed ventrally, the body of the bone is constricted into an elongate hour-glass continuous with a flat plate lying above it. No dermal tooth-bearing bones are associated with any of the basibranchials.

In addition to the toothed fifth ceratobranchials (the lower pharyngeal bones), there is a pair of toothed **upper pharyngeal bones**. The ventral faces of these flat, approximately square bones are densely covered with long teeth. Each bone lies partly below the anterior tip of epibranchial IV of its side (Text-fig. 21), with which it articulates freely. In life, much of the toothed area is apposed to the tooth-patch on the fifth ceratobranchial.

Dr. Nelson (personal communication) is of the opinion that the upper pharyngeal bones of *Denticeps* correspond to the fifth upper pharyngeal tooth plates of clupeoid fishes (U.P. 5 of Nelson, 1967).

Gill rakers are carried on the anterior and posterior faces of all gill-arches except the fifth, where they are found on the anterior face only.

Gill raker counts and distribution in one fish (35 mm. S.L.) are tabulated below; where a raker is situated between two elements of an arch it is shown in that position in the table.   o = gill rakers absent; — = skeletal element absent.

	I		II		III		IV		V	
	Ant.	Post	Ant.	Post	Ant.	Post	Ant.	Post	Ant.	Post
I.P.B.	o	o	o	o	o	o	o	o	—	—
E.B.	4 (1)	5	4 (1)	4	4	4	o	o	—	—
C.B.	7 (1)	4	6	5	7	7	7	9	7	o
H.B.	1	o	3	1	1	o	—	—	—	—

All gill rakers are poorly ossified except near their basal articulation.   Those on the anterior face of ceratobranchial I are long and slender (but well-spaced), while those on succeeding arches are progressively shorter and stouter until, on arch V, they are reduced to low knobs.   Gill rakers on the posterior face of an arch are shorter than those on the anterior face.   Shortest posterior rakers occur on arch I. On this arch the posterior ceratobranchial rakers are almost vertically aligned; on other arches the rakers have a dorsomedial orientation.

PECTORAL GIRDLE

The pectoral girdle of *Denticeps clupeoides* is a substantial structure with expansive cleithra and coracoids.   The pectoral fins, however, are in no way exceptional in size or shape for a fish of this size.

The horizontal part of the *cleithrum* (Text-fig. 23) is longer than the vertical arm, is fairly expanded, and deeply concave in transverse section (the concavity facing inwards).   The vertical limb is short and stout, with the ascending arm produced posteriorly into a thin but expansive shield whose anterior margin extends up about three-quarters of the arm.

The **coracoid** (Text-fig. 23) is also an expansive bone, plate-like and approximately ovoid in outline.   It meets the cleithrum of its side along the entire medial edge of the latter's horizontal arm.   Anterodorsally, the coracoid margin is irregularly serrate, the serrae forming a deeply interdigitating suture with those of the opposite coracoid.   Near the posterior margin there is a thin but broad-based projection which meets the basal expansion of the mesocoracoid.

The **mesocoracoid** (Text-fig. 23) is shaped rather like a fish-hook, the " barb " being directed anteriorly.   It is a flattened but slightly twisted bone, broadest over the area of curvature.   Near the head of the " hook " (where the mesocoracoid articulates with the cleithrum) there is a moderately prominent posterior projection.
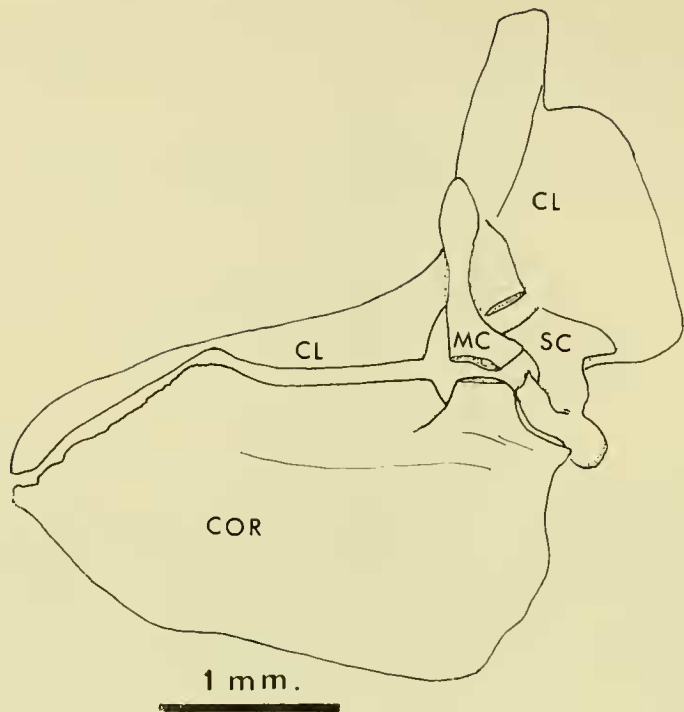
FIG. 23. Pectoral girdle (right half), medial aspect seen from slightly above. The various
elements have separated during treatment and are shown in that position.

The scapula articulates with a broad ridge on the medial face of the cleithrum, near
the junction of its ascending and horizontal arms.

The scapular foramen is very large, with only its posterior margin provided by the
scapula itself.   Its lateral margin is formed from the cleithrum, its anterior margin
from the cleithrum and coracoid, while the inner margin is provided by the coracoid
alone.   No intercalated cartilage was found between the scapula and the other bones
contributing to the boundary of the foramen.

Articulation of the pectoral fin rays (Text-fig. 24).   The pectoral fin is unusual
in having a double row of radials supporting the ventral (i.e. posterior) third of the
fin.   In all, there are two distal and three proximal radials supporting the eleven
(rarely twelve) rays of the fin.

The first ray articulates directly with the scapula over a slight, elongate eminence
between the posterior scapular projection and the more pronounced posteroventral
prominence with which the small second and third rays articulate.

The fourth and fifth rays also articulate (but through a common radial) with the
scapula.   The sixth to eighth rays also share a large, single distal radial which in
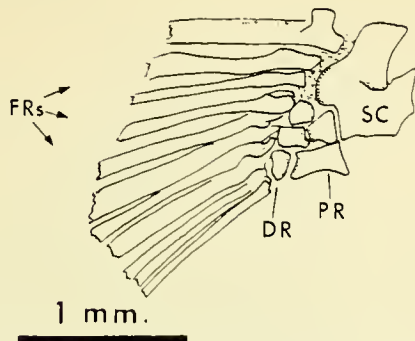
FIG. 24. Articulation of the pectoral fin rays (left side), seen from above with the anteroposterior axis of the fin aligned horizontally.

turn articulates with a capstan-shaped proximal element associated with the mid-ventral area of the scapular margin.

The ninth to the eleventh pectoral rays share a common distal radial which, in turn, articulates with an elongate, rectangular proximal element meeting the coracoid immediately below the scapulo-coracoid junction.

In one specimen examined, there is a twelfth ray, very short and fine; it too shares the same radial as the ninth to eleventh rays.

Dorsal elements of the pectoral girdle. The **extrascapular**, which should be included here, has already been discussed (p. 235) in connection with skull roofing bones. Of the two remaining bones, the **supracleithrum** is firmly attached to the cleithrum. It is a large, flat bone, kidney-shaped in outline with the concave side directed forward. The tube carrying the laterosensory canal from the body passes obliquely across the supracleithrum. It opens into the laterosensory tube of the posttemporal where the latter overlaps the anterodorsal half of the supracleithrum.

The **posttemporal** (Text-fig. 25) has a large, nearly rectangular and flat body, but with the anterodorsal angle greatly produced into a substantial, flattened spine. The tip of this spine is firmly attached to the pterotic and the epiotic. The medial limb of the posttemporal is partly ligamentous; only about the proximal half is ossified. Distally, the ligamentous section is firmly associated with the pterotic at a point slightly below the horizontal semicircular canal, just anterior to the pterotic-exoccipital junction.

The laterosensory tube runs near the ventral margin of the bone, and joins with the lower limb of the extrascapular laterosensory tube. A single row of odontodes runs along at least part of the posttemporal tube.

Postcleithrum. The postcleithrum is probably represented by two small, scale-like bones associated with the upper part of the cleithrum. The superior, and larger, element is nearly circular and is pierced by a tubule of the somatic lateral-line. It lies immediately behind and in contact with the uppermost part of the vertical
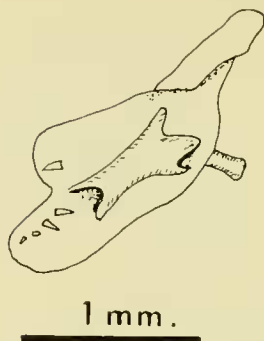
FIG. 25.   Right posttemporal, in dorsolateral view.

cleithrum limb; its ventral tip barely overlaps the dorsal margin of the lower post-cleithrum.

The latter is bean-shaped and relatively elongate; about half of the bone is covered by the posterior, flange-like extension of the cleithrum.

As Clausen (1959) observed, the postcleithra have a striking resemblance to body scales, the upper even showing traces of what appear to be annuli.

AXIAL SKELETON

Vertebral column (Text-figs. 26–29).   There are forty vertebrae (including the small second ural centrum) in the column of the three specimens examined, and in three others that were radiographed.

All the vertebrae are well-ossified; excepting the first abdominal and the second ural centra, all have the neural and haemal arches firmly fused to the centra, and are amphicoelous.   Again excepting the first abdominal centrum, all centra are pierced by a narrow but distinct notochordal foramen.

Intermuscular bones are present (save for the first vertebra) along the entire length of the column.   Over about its anterior half only epipleurals or epicentrals are present, but over the posterior half both dorsal and ventral intermusculars are developed; for a short section all three types of intermuscular bones are present.

The **first abdominal vertebra** (Fig. 14) is reduced and very firmly attached to the skull.   The anterior face of the centrum is rough and clearly divided into three facets corresponding to the occipital condyle of the skull (see p. 233).   The long, slender neural arches are autogenous; their somewhat expanded distal ends do not meet in the midline.   No intermuscular bone is associated with this vertebra.

The **second vertebra** is slightly shorter than the third (Text-fig. 26).   It has a fully developed neural spine and arches.   Immediately above the spinal cord, the arches curve medially and almost meet, thus roofing the cord at this point.   Because the proximal ends of the neural spine are widely separated, a space is formed above the spinal cord roof.
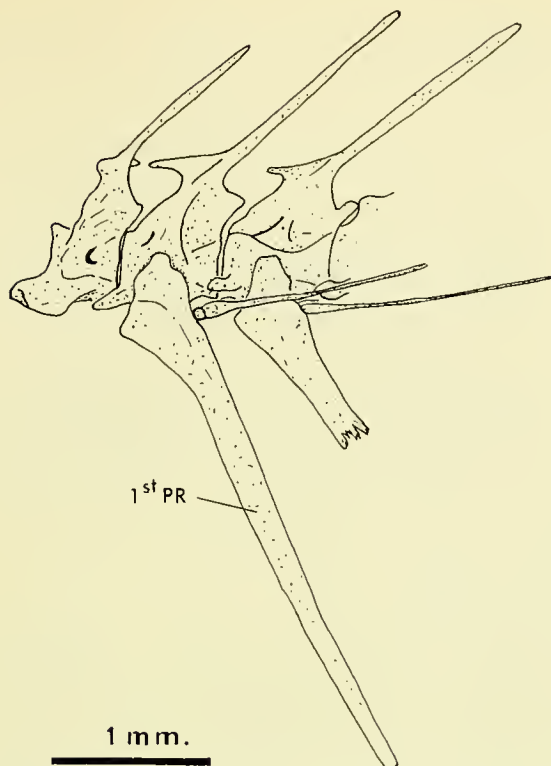
FIG. 26. Second to fourth abdominal vertebrae, left lateral view.

A broad, anteriorly directed process arises ventrolaterally from each side of the centrum, and projects slightly beyond its anterior face. As the tips of these processes are turned inwards, they effectively embrace the posterolateral aspect of the first centrum.

I am uncertain as to the identity of these processes, but because the intermuscular bone (which in the more posterior and rib-bearing vertebrae articulates with a rib) is joined to the process, it could be an enlarged parapophysis fused with the centrum.

No pleural rib is associated with this vertebra, but an epicentral intermuscular bone is present.

Abdominal vertebrae 3–14: all carry well-developed pleural ribs which articulate directly with the centrum except on the fourteenth vertebra. Here there is an autogenous parapophysis-like structure which closely resembles the head of the rib on other vertebrae; it also bears the intermuscular bone.

All vertebrae in this section of the column are similar in form. The long-based

neural arches almost meet medially above the spinal cord, and are capped by the bifurcate base of the neural spine. On the third and fourth vertebrae the medial shelf is produced anteriorly so as almost to meet the preceding vertebra. This anterior projection is much shorter in the other vertebrae, and is barely recognizable on the fourteenth vertebra.

Short dorsal pre- and postzygapophyses are present. Ventrally there is a prezygapophysis-like projection curved medially and contacting the posterior face of the preceding centrum. The process increases in size anteroposteriorly and becomes increasingly involved in the articulation of the pleural ribs. From the tenth vertebra backwards, the greater part of the rib head is in contact with this process, although the rib still has a distinct articulation with the centrum. Because of this relationship with the rib, I would identify these projections as parapophyses fused with the centra.

The **pleural ribs** (of which there are twelve articulating pairs, and two floating pairs) are long and substantial bones with deep, somewhat concave heads merging indistinguishably with the broad proximal part of the rib (Text-fig. 26). Each rib articulates directly with the centrum; a well-defined articular boss on the upper part of the head fits into a deep pit in the centrum. The articulation with the presumed parapophysis mentioned above is effected through the anteriorly curved ventral margin of the head.

The fine, slender and unbranched **epipleurals** are attached to the ribs near their articulation with the centrum.

Ventrally, the distal tips of the ribs contact the medial line of scutes. Clausen (1959) states that the ends of the ribs join the scutes " . . . causing the ribs to form a complete hoop exactly as the similar scutes in many Clupeidae ". I have been been unable to confirm this in the specimens I examined. In these the scutes are free and merely touch (but to not join) the ribs. The scutes are without a distinct ascending arm.

The **fifteenth vertebra** has a short haemal arch which arises from the base of what appears to be a short parapophysis fused with the centrum (and with which the epicentral intermuscular bone articulates).

Immediately below this vertebra are a pair of short but otherwise fully-developed ribs, closely resembling their anterior congeners except for having attenuated and not truncated ends. In an alizarin transparency this rib pair seems to " float " in the hypaxial musculature (see Text-fig. 27).

The **sixteenth vertebra** is similar to the fifteenth but has a more expansive, plate-like haemal spine. It too has a pair of " floating ribs " and an epicentral articulating with the parapophysis.

The **seventeenth vertebra** (or using Nybelin's [1963] nomenclature, the twenty-second preural) is the first true caudal vertebra. From this point until the first ural vertebra all vertebrae are of a generally similar form, with long, slender haemal spines.

The neural arch of all preural vertebrae is long-based, a transverse supraneural shelf is present (as in the abdominal vertebrae) but the aperture above it, formed between the bases of the neural spine, becomes progressively smaller caudad. From
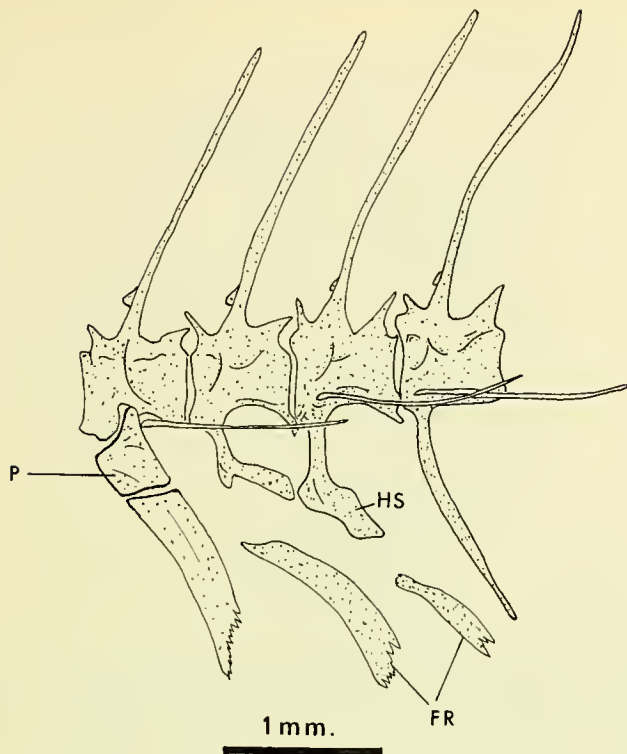
FIG. 27. Transition between abdominal and caudal vertebrae, showing the last pleural rib, its parapophysis-like process (P), and the two " floating " ribs (FR); left lateral view.

the fifth to the first preural, the shelf is absent and consequently there is only one aperture between the centrum and the neural spine.

Preural vertebrae 3 to 5 have a longer haemal arch base than do the preceding elements, and a foramen is present in it. The neural spines of preural vertebrae 2–5 are expanded anteroposteriorly, but that of preural 1 is greatly reduced. Haemal spines of preural vertebrae 1–6 are also expanded, that of preural 6 only slightly so, and that of preural 2 greatly expanded (more so even than the haemal spine of preural 1; see Text-fig. 29).

Equally developed dorsal pre- and postzygapophyses are present on the more anterior preural vertebrae, with the prezygapophysis becoming slightly larger on the posterior vertebrae.

Ventral postzygapophyses are developed on the anterior preural vertebrae, but in the posterior elements a prezygapophysis-like process is developed from the base of the haemal arch as well. This process does not, however, directly contact the ventral postzygapophyses of the preceding vertebra.
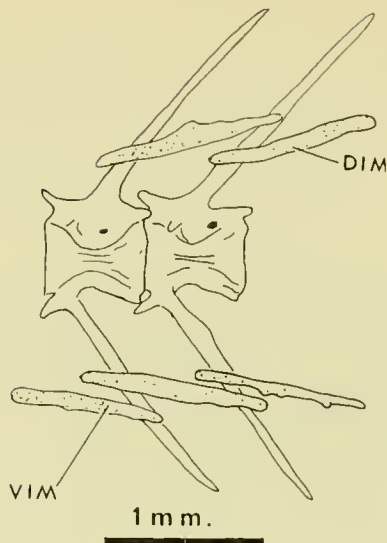
FIG. 28.   Caudal vertebrae (preurals 14 and 15), left lateral view.

Epicentral intermuscular bones are associated with preural vertebrae 22 to 15.
Dorsal intermuscular bones (Text-fig. 28) first appear above the eighteenth
preural vertebra.   The first few dorsal intermusculars are fine, short and branched;
they become progressively larger and longer but the short upper limb is not
developed in about the posterior half of the series (Text-fig. 28).   The last dorsal
intermuscular bone lies above the second preural vertebra.   **Ventral intermuscular
bones** first appear below the twentieth preural vertebra, and are stouter than their
dorsal counterparts which they otherwise resemble.   The lower limb is absent in
bones from the posterior half of the series.   The last ventral intermuscular bone is
associated with the fourth preural vertebra.

CAUDAL FIN SKELETON

The caudal skeleton (Text-fig. 29) is one of the most characteristic features of the
Denticipitidae.   Although undoubtedly of the clupeomorph type (see Gosline, 1960,
1961; Greenwood *et al.*, 1966) it differs from all known living and fossil clupeomorphs
(including *Diplomystus* and *Knightia*).   Like several other features of the denti-
cipitids, the caudal skeleton is a mosaic of primitive and specialized features.

Five vertebrae are involved, namely: two urals (U1 and U2) and the first three
preurals (PU1–3).   Five hypurals are present, and there are two epural bones.   A
single uroneural is present on each side.   The axis of the skeleton curves gently and
evenly upwards through four vertebrae (PU1–2, U1–2).

In addition to the eighteen principal caudal rays (comprising one unbranched
and eight branched rays in each lobe) there is an upper and two lower procurrent rays
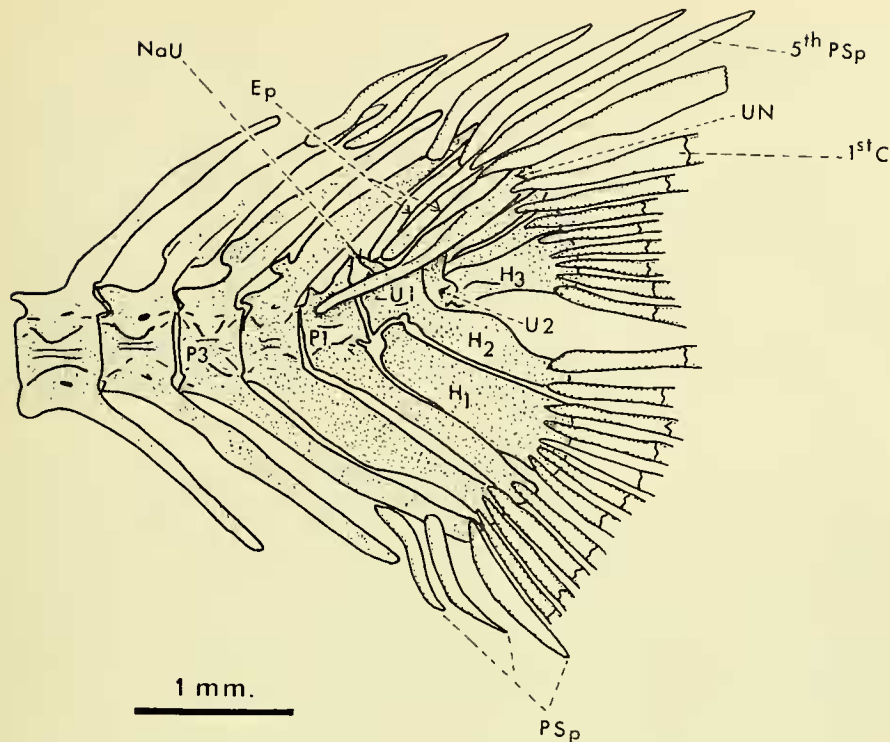
FIG. 29. Caudal fin skeleton. Intermuscular bones removed for clarity. Left lateral view.
PI–3 : first to third preural vertebrae.

(short, but segmented distally) and a series of procurrent " spines ", five dorsally and three ventrally (Text-figs. 29). These " spines " have a deeply divided base, but cannot be separated into left and right halves. Each dorsal procurrent " spine " is articulated with a single vertebral element (the first with the neural spine of PU4 the second with PU3, the third with PU2, and the remaining two with the two epurals), The three ventral spines, however, all articulate with the expanded haemal spine of the third preural vertebra.

Both dorsally and ventrally, the procurrent " spines " increase in length towards the fin, thereby forming a graded series with the segmented procurrent ray preceding the first and last (unbranched) principal caudal rays. These three procurrent rays are segmented distally, but the proximal portion resembles that of a " spine ". Thus, it seems certain that the spines are merely modified procurrent rays.

The **first preural centrum** (PUI) is slightly longer than the second (Fig. 29). Its neural arch is complete but very narrow-based and short, the neural spine showing a correspondingly great reduction in length to little more than a slight spur. The

haemal spine is expanded but less so than that of the second preural vertebra.
There is a well-developed but low hypurapophysis near the base of the spine.

The **first ural vertebra** (U1) has a well-developed centrum, slightly longer than
that of PU1 (see Text-fig. 29). The neural arches, however, are greatly reduced
spurs which do not meet in the midline. In one specimen the arches of each side
are of a different size and shape, one directed anteriorly, the other posteriorly.

The **first hypural** has a broad articulation with the anterior half of PU1, but it
is clearly autogenous (Text-fig. 29). **Hypural 2**, however is indistinguishably
ankylosed with the centrum over almost its entire posterior half. Both these
hypurals are broad, the first somewhat more so than the second, and also slightly
longer. The posterior margin of hypural 2 is deeply excavated over the distal half
in some specimens, but less markedly so in others.

The **second ural vertebra** (U2) is reduced to a short, rather wedge-shaped
centrum. Like the other centra, it is penetrated by a distinct notochordal foramen
which in this centrum leaves near the posterodorsal margin.

Hypurals 3 to 5 articulate with the posterior face of the second ural centrum
(Text-fig. 29). Hypural 3 is relatively broad, and its dorsal margin is closely applied
to the ventral margin of hypural 4; in one specimen these two hypurals appear to
be fused, but with the line of fusion still evident. Hypural 5 is narrow and clearly
separated from Hypural 4; it is partly obscured proximally by the uroneural.

Each of the paired **uroneurals** (Text-fig. 29) is a long, strap-like and thin bone,
firmly articulated with the first preural vertebra through a pit on its anterodorsal
surface; although the articulation is firm, the bones are not fused. Above the
second ural centrum, the dorsal margin of the uroneural is slightly expanded. Beyond
this point, the uroneurals meet medially and are closely apposed but not fused for
the remainder of their length.

The two **epurals** (Text-fig. 29) are slender and elongate. The first epural contacts
the aborted neural arch of the first ural centrum, while the second epural touches the
base of the first a little above its point of articulation with the neural arch. The
fourth and fifth procurrent " spines " articulate with the two epurals respectively,
and the proximal tip of the upper procurrent ray articulates with the second epural.

SKELETON OF THE MEDIAN FINS

The short **dorsal fin** is supported by seven pterygiophores. The first has a broad
distal base and carries two rays. The remaining pterygiophores have a similar
shape but decrease in size posteriorly. Each supports only one ray. The first
dorsal ray articulates directly with the pterygiophore head but all other rays have a
small radial (presumably the distal) interposed.

The relationship of pterygiophores to vertebrae is rather irregular and shows some
individual variability, but with at least one instance in each fish of two pterygio-
phores situated between a pair of vertebrae.

The long **anal fin** is carried by twenty-two pterygiophores. The first has three
rays (two unbranched and unsegmented) and a relatively long head. Its two un-
branched rays lack an intermediate radial, but a radial is present at the base of all

other anal rays. The first pterygiophore articulates proximally with the posterior face of the broad but short haemal spine carried by the twenty-second preural vertebra. The remaining twenty-one pterygiophores are of similar shape, and each supports one branched ray, except the last, which carries two (but both sharing one radial).

In the anal fin, as in the dorsal, there is a variable relationship between the pterygiophores and the vertebrae. However, in this fin there is a higher incidence of two pterygiophores per vertebral pair. For example, two specimens each have seven cases of such pterygiophore pairs, but different pairs of vertebrae are involved.

Interneurals are present between the tips of neural spines 2 to 11 (i.e. between the third to twelfth vertebrae). The first five interneurals are fairly broad and somewhat boomerang-shaped bones which contact the neural spine a short distance from its tip. The remaining interneurals are more slender and splint-like; all are poorly calcified.

PELVIC GIRDLE

The two halves of the girdle lie below the sixth to seventh pairs of ribs, which are shorter than those preceding and following them.

Each half of the girdle is a long, slender, and poorly ossified bone; in outline they are triangular, in cross-section somewhat curved. The two halves are closely apposed medially, at an angle of about 45° to the vertical, but only in contact at the ischial region. Lateral to the point of contact, the girdle is rather bulbous in section.

Two cuboid radials of approximately equal size articulate with the posterior, face of the bulbous section. The inner radial may represent two fused elements, a small inner and a larger outer one, if a densely staining vertical bar represents a line of fusion. The innermost pelvic fin ray is moveably articulated with this radial (see Gosline, 1961).

On the upper surface of the ischial swelling there is a stout L-shaped ossicle, lying with one arm closely but moveably applied to the bone. The tip of the upper half of the first pelvic ray articulates with the posterior face of this ossicle. Articulating with its dorsal face is a small plate of slightly calcified bone lying parallel to the long axis of the girdle (Text-fig. 30). In life this plate is embedded (albeit super-
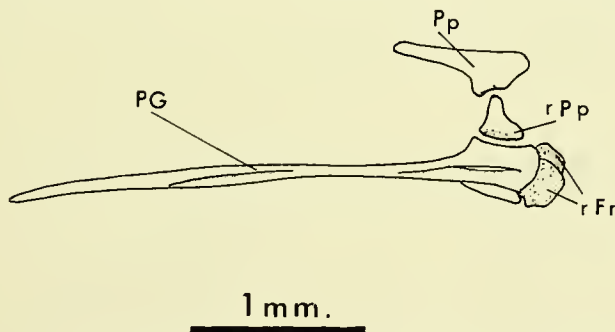

1 mm.

FIG. 30. Pelvic girdle and associated pelvic plate of the right side in medial view.

ficially) in the body muscle; I have been unable to trace any ligamentous connection between the plate and any part of the pelvic girdle or fin.

The plate is variable in outline, and can even be of a different shape on either side of one fish. Basically, however, it is anvil-shaped, with the foot directed ventrally and always clearly formed into an articulatory surface.

Whitehead (1963a) identified this enigmatic bone as a pelvic scute, and suggested that it represented an early stage in the evolution of a typical clupeoid pelvic scute from a pelvic splint bone. He did not realize at that time that the bone was articulated, through a radial-like element, with the pelvic girdle.

I find difficulty in accepting Whitehead's interpretation (see below), partly because of the articulation, and partly because the pelvic scutes in other clupeomorphs are so similar to abdominal scutes. Admittedly, the presence of the pelvic scutes in otherwise scuteless forms requires explanation, and at present such an explanation is not readily forthcoming. It seems, however, that the answer will only be found when more is known about the phyletic history of the Clupeomorpha. An aspect of this history particularly relevant to the scute problem is whether or not the earliest clupeoids were scuted, and if they were, what was the nature of the scutes.

The abdominal midline in *Denticeps* is covered by a single row of transversely V-shaped and deeply keeled scales which can certainly be considered scute-like (Text-fig. 31). The scales do, however, differ from typical clupeoid scutes in lacking a protracted ascending arm. But, could not the *Denticeps* abdominal scute-scale represent an early stage in scute evolution? The arm could develop through differential growth of the upper margin.
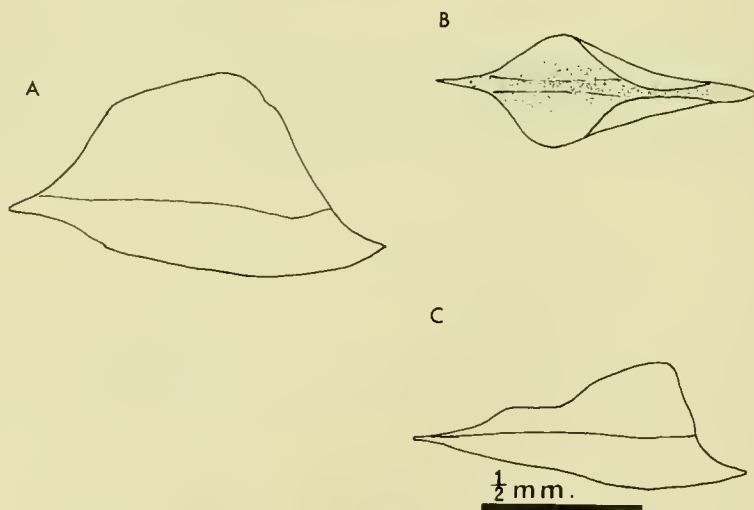

Fig. 31. Ventral scutes. (A) Abdominal (prepelvic) scute in left lateral view (B) Pelvic scute from above, anterior to the left. (C) Pelvic scute in left lateral view.

In *Denticeps* there is no break in the continuity of abdominal scute-scales at the pelvic fin base. However, the scale between the fins is shorter, and of a different form. Whereas the others are of a simple U or V cross-section with the arms diverging, the pelvic scale is dorsally constricted over its posterior half. As a result, the arms almost meet medially. The anterior half also differs since the arms do not rise steeply but lie almost horizontally. (Text-fig. 31B). The constricted part of the scale fits closely behind the conjoined halves of the pelvic girdle, while the nearly horizontal forward section lies immediately anterior to the base of the innermost fin rays. Indeed, seen *in situ*, this scale closely resembles the medial part of the pelvic scute in *Spratelloides delicatulus* figured by Whitehead (*op. cit.*, fig. 2b.). Lateral and dorsal growth of the anterior part of the *Denticeps* scale would produce a *Spatelloides* type of scute.

Thus, I would suggest that the pelvic scute in clupeoids is derived from an abdominal scute (through perhaps, a stage of scute-scale) and not from a pelvic splint bone as Whitehead (1963a) argues. It this is so, then the bony pelvic plate of *Denticeps* is another structure altogether, and one not directly connected with the evolution of pelvic scutes in the template-model fashion that Whitehead postulates.

No other clupeomorph fish appears to have a pelvic plate like that of *Denticeps*, and its identity and homology are not obvious. A lateral pelvic plate, possibly articulating with the girdle, occurs in an atheriniform fish identified by Sewertzoff (1934) as *Belone acus*. I have dissected a specimen of *Belone belone* (probably the species actually seen by Sewertzoff) and find that although there is a vertical plate associated with the ischial region of the girdle, it appears to be continuous with the girdle and not moveably articulated, (which is what I take Sewertzoff to mean when he describes it as " gelenkig verbunden "). Sewertzoff (*op. cit.*) was unable to identify the plate in *Belone* with any other structure in the teleostean pelvic girdle, and concluded that " Es ist eine Neubildung ". But, if it is not a separate ossification, then it would seem to be merely a localized hypertrophy of the girdle. Similar plates are found in species of *Scomberesox* (personal observation), and a flattened or stylar process occurs posterolaterally from the girdle in many exocoetids, scomberesocoids and adrianichthyoids (Rosen, 1964).In all these fishes, the process is continuous with the girdle.

The situation in *Denticeps*, where there is a distinct articulation (through a radial-like ossicle) between plate and girdle, does not seem to be comparable with the atheriniform condition described above. Rather it invites comparison with the radial and the proximal end of a pelvic fin ray.

Could it perhaps be, as Whitehead suggested, homologous with the pelvic splint bone found in a number of lower teleostean fishes (Gosline, 1961; Patterson, 1964) but not in the Clupeoidei (Whitehead, 1963a)? Pelvic splints are usually unpaired bones (*Albula* is apparently exceptional, see Whitehead, *op. cit.*), lying asymmetrically to the fin axis, and not having direct contact with the girdle. Patterson (*op. cit.*) believes splint bones to be derived from fulcral scales, and is the only author to express views on their origin. If Patterson's interpretation is correct (but he admits it is only speculative) then the pelvic plate in *Denticeps* is unlikely to represent the remnants of a pelvic splint. Unless, of course, it is a fulcral scale that has sunk

further into the body than is the case with typical splint bones, and developed a sesamoid radial articulation with the girdle.

On the other hand, if pelvic splints are reduced fin rays which have lost their basal articulation with the girdle, *Denticeps* could represent another trend. That is, one in which the basal articulation is retained but the distal portion of the ray, and most of its head, is lost (see below).

Without more fossil and comparative histological evidence it is impossible to develop either suggestion further. Whatever the outcome, the pelvic plate in *Denticeps* remains an unusual and highly characteristic structure.

Another unusual feature of the pelvic fin is its branched outer (i.e. first) ray, distinguishable from the other four rays only by its slightly greater length. Branched first pelvic rays are of rare occurrence amongst teleosts, but are recorded from two distantly related families, the Astronesthidae (Stomiatoidei) and Aphredoderidae (Percopsiformes). The absence of an unbranched and relatively enlarged first ray in *Denticeps* (together with the low pelvic ray count), coupled with presence of the pelvic plate, might suggest that the plate represents an aborted first ray.

ADDITIONAL NOTES ON THE OSTEOLOGY OF *PALAEODENTICEPS TANGANIKAE* GREENWOOD 1960

Since the original description was published (Greenwood 1960) I have been able to examine four more specimens from the same deposits (at Singida, Tanzania). This material, together with the better knowledge I now have of the living genus, enables me to reinterpret certain features of the fossils. In turn, this has led to a rediagnosis of the genus *Palaeodenticeps*.

Recent work on other fossil fishes from the same beds as *Palaeodenticeps tanganikae* also suggests that the genus may be somewhat older (possibly Oligocene) than the Miocene date at first supposed (see Greenwood & Patterson, 1967).

Thus, the original description of *P. tanganikae* can be amplified and amended as follows:

Syncranium. In the holotype of *P. tanganikae* (B.M. [N.H.], reg. no. P. 42610), part of the pterotic can be recognized (see pl. 2 in Greenwood, *op. cit.*). It shows the two large, contiguous openings for the infraorbital and preopercular laterosensory canals just as in *Denticeps clupeoides*. Immediately behind the pterotic fragment there is an almost entire extrascapular, which differs little from that of *Denticeps*.

An elongate fragment of bone lying in the orbit of the holotype is almost certainly not the supraorbital (see fig. 2, p. 7, Greenwood, *op. cit.*). The supraorbital of *Denticeps clupeoides* is a small, cuboid bone situated anteriorly in the orbit (see above, p. 224). There is the possibility that the bone is the supraorbital ledge of the frontal, which Clausen originally identified as the supraorbital (see p. 224). However, the ledge carries a row of strong odontodes; these are not visible in the fossil, and the bone does not have the pitted appearance of a surface which has lost its odontodes. I am, therefore, now inclined to identify the bone as part of the

orbitosphenoid, probably its ventral margin. Certainly its position relative to the skull roof and to the parasphenoid does not negate this new interpretation.

That the posteroventral preopercular " spine " is shorter in *Palaeodenticeps* than in *Denticeps* is confirmed by the additional material. The large depression situated near the base of the vertical arm of the preoperculum in *Palaeodenticeps* (Greenwood, *op. cit.*, p. 7) is apparently equivalent to the upper posterior opening in *Denticeps* (see p. 238 above). Its greater prominence in *Palaeodenticeps* may be correlated with the shorter " spine " in that genus.

Palaeodenticeps was thought to differ from *Denticeps* in having a " toothed " suboperculum but it is now known that odontodes also occur on this bone in *Denticeps* (see p. 240).

Jaw structure in both genera appears to be remarkably similar, although there are fewer maxillary odontodes in *Palaeodenticeps*. My earlier remarks about fewer odontodes on the dentary of the fossil are not confirmed by the new material.

The bone tentatively identified as a urohyal in the holotype now seems more likely to be the dentary of the left side protruding from under the right dentary (Greenwood, *op. cit.*, fig. 2 and pl. 2). If it is the urohyal, then it is a much stouter bone than in *Denticeps*.

Axial skeleton. The marked difference in the number of vertebrae characterizing the genera (thirty-one or thirty-two in *Palaeodenticeps*, cf. forty in *Denticeps*) is confirmed by the additional fossils, all of which have thirty-two vertebrae. Undoubtedly correlated with these differences is the fact that there are ten pairs of attached pleural ribs in *Palaeodenticeps*, and twelve pairs in *Denticeps*. Both genera have two pairs of " floating ribs " associated with the ultimate and penultimate abdominal vertebrae (and not three pairs as I indicated in the original description of *Palaeodenticeps*).

There is close similarity in the caudal fin skeleton of both genera. The difference in the number of upturned vertebrae, which I noted in 1960, is probably of no significance since in *Denticeps* there are only two vertebrae showing distinct inclination (ural I and II), as is the case in *Palaeodenticeps*.

The size, shape and relationships of the single uroneural are identical in both genera. In my description of *Palaeodenticeps*, I implied, by using the words " ultimate uroneural ", that another was present. It is now clear that only one uroneural is present in *Palaeodenticeps*, and that it extends further posterodorsally than I described.

Unfortunately, it is still not possible to determine the number of epurals present in the fossils. In the holotype there appear to be two epurals, but in another specimen (from Sheffield University) three seem to be present.

This Sheffield University specimen clearly shows that the first hypural is free from the ural centrum, and that there are three hypurals in the upper lobe of the caudal fin skeleton (that is, just as in *Denticeps*).

Contrary to my original counts, the number of principal caudal fin rays in both *Denticeps* and *Palaeodenticeps* is identical, i.e. eight branched and one unbranched ray in each lobe of the fin. Both genera also have the same number of spinous procurrent rays.

Pectoral girdle.   No further information is available on the postcleithrum of *Palaeo-denticeps* (see Greenwood, 1960, p. 6), and the possible generic differences in this structure must remain an open question.

DISCUSSION.   When this new information is taken into account it is necessary to redefine the genus *Palaeodenticeps* as follows: a member of the family Denticipiti-dae, differing from the extant genus *Denticeps* in having fewer vertebrae (thirty-one or thirty-two cf. forty), lateral line scales (thirty-two or thirty-three cf. thirty-seven to forty) and pleural ribs (ten pairs cf. twelve), and in having the origin of the dorsal fin above or slightly anterior to the first anal fin ray.

The resemblances between *Denticeps* and *Palaeodenticeps* are now seen to be closer than was previously realized.   Possibly the two genera should not be maintained. However, as judged by the criteria employed in the systematics of extant clupeoids, generic status is justified.   From the evolutionary viewpoint the morphological differentiation that took place in the family between Palaeogene (probably Oligocene) times and the present is of a fairly low order.

RELATIONSHIPS AND CLASSIFICATION OF THE DENTICIPITIDAE

Neither Clausen (1959) nor Greenwood (1960) paid more than passing attention to the systematic position of the Denticipitidae.   Clausen, at least implicitly con-sidered that the family has decided clupeoid affinities.   He also stated that it had many features in common with the Elopidae, Albulidae and Osteoglossidae.

I can find no grounds for maintaining the suggested affinity with the Elopidae and Albulidae (or for that matter with the Megalopidae).   Clausen (*op. cit.*) probably thought that the supposed medioparietal condition of *Denticeps clupeoides* was elopoid; but, as is now known, the parietals are not in contact (see p. 235).   Green-wood *et al.* (1966) stated that the caudal fin skeleton of *Denticeps* " . . . approaches the condition of the elopiforms . . .".   This view too must now be abandoned since it was based on insufficient detailed knowledge of the skeleton.   As will be discussed later, the denticipitid caudal skeleton is definitely clupeomorph, albeit somewhat different from the typical condition seen in extant clupeoids.

In both general and detailed skull morphology, the denticipitids are far removed from the elopoids.   Likewise there are no significant points of resemblance in the branchial skeleton.   The specializations of the denticipitids in both these systems make it impossible even to suggest any close relationships with the more primitive elopoids.   The articulation of the upper jaw elements is similar in both groups, but since the condition is a primitive one, it is of little value as a phyletic indicator.

Possible denticipitid-osteoglossid relationships are difficult to substantiate, but relationships with the Osteoglossomorpha as a whole are possible.

At first sight, the enlarged, partially contiguous nasals of the denticipitids resemble the osteoglossid condition.   But, there are differences in detail which con-siderably reduce the resemblance (for instance, their suprafrontal situation, medial contact confined to the hind limits, and their flimsiness).   In fact, it is difficult to visualize how the denticipitid condition could be related to any evolutionary stage leading to or from the osteoglossid condition.

There is, however, a greater resemblance between the nasals of *Denticeps* and those of certain notopteroid fishes (currently classified in the Osteoglossomorpha), a resemblance probably correlated with the existence of open, gutter-like supraorbital laterosensory canals in both groups (Greenwood, 1963). The phyletic significance of this similarity in the cephalic laterosensory system is not fully apparent, especially since the denticipitids and notopterids both differ from and resemble one another in several other cranial characters. If these resemblances have any phyletic significance, they must be of great antiquity because both lines have now evolved away from one another to a considerable degree.

The relationships of upper jaw elements (including the palatine) to each other and to the skull, are rather similar in the denticipitids and osteoglossids. But, since this arrangement is a very simple one (especially in *Denticeps*) and presumably is primitive, no phyletic importance can be attached to it. In other orobranchial characters the two families are very dissimilar, and the dissimilarity can be extended to include all osteoglossomorphs (see Greenwood *et al.*, 1966; too little is known about the orobranchial region in the recently discovered fossil, *Singida jacksonoides*, to include it in this generalization [see Greenwood & Patterson, 1967]).

Similarly, there are very few resemblances in neurocranial architecture; the Osteoglossidae retain a primitive structure including a well-developed basipterygoid process. Other Osteoglossomorpha (Notopteroidei and Mormyriformes) show a more specialized level of neurocranial organization, but these specializations are not of the type found in the Denticipitidae (excepting, perhaps, the cephalic laterosensory canal system in certain Notopteroidei).

There is a noticeable resemblance between the preoperculum in denticipitids, especially *Palaeodenticeps*, and certain osteoglossids (especially *Scleropages* and *Osteoglossum*, to a lesser extent *Arapaima* and *Heterotis*), the Singididae and the Notopteridae. In all these fishes the entire ventral limb of the preoperculum is virtually an enlarged laterosensory canal with several ventral openings arranged in a straight line, and with the inner face of the bone projecting beyond this line. Often there is a large opening near the junction of the horizontal and vertical preopercular arms, and the posteroventral margin may be protracted.

This type of preoperculum cannot be considered truly primitive. Rather, it is a derivative of the primitive type found in *Thrissops* and its allies (Nybelin, 1964, 1967). That it occurs in such otherwise dissimilar groups as the Denticipitidae and certain Osteoglossomorpha may be significant as an indicator of distant relationships between the groups. It would be on a par, phyletically speaking, with the notopterid-denticipitid similarities in cephalic lateral-line arrangements (see above).

The short parasphenoid of *Denticeps* is another osteoglossid-like feature (but a short parasphenoid also occurs in the Engraulidae among the clupeoids), as is the direct articulation between rib head and centrum (Greenwood, 1963). Neither of these characters has been sufficiently studied amongst teleosts to assess their significance.

The types of caudal fin found in the known Osteoglossomorpha are characteristic (see Greenwood, 1967, Greenwood & Patterson, 1967, Greenwood *et al.*, 1966), and do not appear to be closely linked with the clupeomorph type to which the denti-

cipitid caudal clearly belongs. However, all could be derived from the *Thrissops-Allothrissops* type (see Patterson, 1967).

Other osteoglossid-like characters of *Denticeps* which Clausen (1959) noted are the loss of supramaxillae, and the position of the median fins. The relative position of the dorsal and anal fins is unlikely to be of value in determining phylogenies. Although loss of the supramaxillae is certainly a specialized feature in both groups, I do not know what value to attach to it.

To summarize: there are certain characters, all of a specialized or derived nature, common to the Denticipitidae and the osteoglossomorph fishes. The nature of these characters, taken in concert with those in which the two taxa differ, strongly suggests that if any phyletic connection exists between them it is a distant one, possibly from as far back as the level represented by the Jurassic genus *Thrissops*.

The clupeomorph affinities of the Denticipitidae, in contrast, are clear, although the relationships of the family with the Clupeoidei are somewhat obscure.

The living Clupeomorpha are trenchantly defined on the basis of three character complexes (Greenwood *et al.*, 1966), namely: (i) The presence of intracranial swimbladder diverticula encased in bony bullae developed in association with either the prootic and pterotic bones, or the prootic alone; the prootic bulla is intimately associated with the utricular recess. (ii) An intracranial space, the *recessus lateralis*, into which open the major cephalic laterosensory canals as well as the temporal canal; the *recessus* is separated by a membranous fenestra from the perilymphatic spaces of the ear (see Wohlfahrt, 1936). (iii) The caudal fin skeleton (see below; also Hollister, 1936; Gosline, 1960, 1961; Greenwood *et al.*, 1966, and Cavender, 1966).

To the best of my knowledge, none of these characters (either singly or in combination) has been found in any other teleostean group (see also Greenwood *et al.*, *op. cit.*).

The intracranial swimbladder diverticula of *Denticeps clupeoides* are typically clupeomorph in their basic morphology and interconnections with each other and with the inner ear. What differences there are between *Denticeps* and other clupeomorphs are concerned with the relative sizes of the bullae.

The *recessus lateralis* in *Denticeps* is particularly interesting because, compared with the typical clupeoid condition, it is incomplete in not having a separate opening for the supraorbital laterosensory canal (see p. 231).

In clupeoid fishes a posterior extension of the frontal carries this canal backwards to open into the *recessus* (which is bounded by the pterotic and sphenotic, and partly roofed by the frontal) in an anteromedial position. In *Denticeps* the frontal canal ends short of the *recessus*, and external to it. It is, however, connected to a *recessus* opening (that for the infraorbital canal) through the tubular dermosphenotic (see Text-fig. 4). The dermosphenotic (i.e. the uppermost infraorbital bone) in cluepeoids carries the infraorbital canal and opens into the *recessus* through a separate foramen. Thus, *Denticeps* cannot be said to have a typical clupeoid *recessus lateralis*. But, apart from the shared supra- and infraorbital openings (and the correlated difference in frontal morphology) the *recessus* is like that of the clupeoids, and includes a fenestral connection with the perilymphatic system.

Nothing is yet known about the evolution of the clupeoid *recessus*. It is apparently

not developed in *Diplomystus*, at least in those species which have been studied in detail (see Patterson, 1967). The Cretaceous species *D. brevissimus* figured by Patterson (*op. cit.*) seems to have a superficial temporal lateral-line canal, and the infraorbital and preopercular canals are well-separated from one another proximally. By analogy with living clupeoids these details suggest that the *recessus* was not developed. Also significant is the well-developed, large and flat dermosphenotic in *Diplomystus brevissimus*. Its relationships with other canal-bearing bones of the postorbital region are quite unlike those of the dermosphenotic in extant clupeoids or *Denticeps*, again suggesting the absence of a *recessus*.

Possibly *Denticeps* (and *Palaeodenticeps*, see above, p. 258) represent an advanced stage in *recessus* evolution but one differing in detail from the clupeoid evolutionary pattern. That is, it has reached a point at which the *recessus* has developed and, as it were, captured the cephalic canals save for the supraorbital one. The dermosphenotic, primitively linking both the supraorbital and infraorbital canals with the temporal canal (Gosline, 1965), still serves this function, albeit somewhat indirectly. In fact, it is more closely associated with the supraorbital than with the infraorbital canal. The clupeoid pattern, on the other hand, could have developed through essentially this stage, but diverged as a result of the dermosphenotic becoming more closely associated with the infraorbital canal, the supraorbital canal developing an independent opening into the *recessus*. The dermosphenotic continued to link the infraorbital and temporal canals but via the *recessus*.

The caudal fin skeleton of extant clupeoid fishes (at least when adult) is a very characteristic structure, in itself diagnostic for the group. Its principal features are as follows: (i) Hypural 1 is completely separate from the first ural centrum, and is usually separated from it by a distinct gap. (ii) The first ural centrum is greatly reduced in size, sometimes to little more than an enlargement at the base of hypural 2, which is always indistinguishably fused with it. (iii) The second ural centrum is always present (probably fused in with the posterior ural centra if these are present). (iv) The first uroneural extends anteriorly to the first preural centrum, and fuses with it (two other uroneurals are present). (v) The neural spine of the second preural centrum is elongate, its tip reaching to the same level dorsally as that of the third preural vertebra; a procurrent ray articulates with its tip.

In most clupeoids the parhypural (haemal spine of the first preural vertebra, equivalent to the first hypural in Gosline's [1960, 1961] terminology, and Hollister [1936]) is autogenous but closely articulated with the centrum. It may, however, be fused with the centrum in some Dussumieridae (Gosline, 1960). Certain dussumierids may also provide another exceptional condition, namely the fusion of the first ural and preural centra (see Hollister's [1936] figs. 42–44. of *Jenkinsia*).

The denticipitid caudal skeleton differs somewhat from the clupeoid type but is clearly related to it in general plan and in detail (Text-fig. 29, p. 253). Hypural 1 is autogenous but still articulates with the first ural centrum. The articular head is, however, markedly narrower than the proximal part of the hypural body. Hypural 2, like that of the clupeoids, is fused indistinguishably with the centrum. Compared to clupeoids, the centrum of the first ural vertebra in denticipitids is large, in fact only a little smaller than the first preural centrum. As in the clupeoids, a second

ural centrum is present as a reduced structure. The first (and only) uroneural extends forward to the first preural centrum. Unlike the first uroneural of clupeoids, the uroneural in denticipitids does not fuse with the centrum, but fits into a pit on its dorsolateral face. No trace of more than one uroneural could be found in *Denticeps* or *Palaeodenticeps*. Like the clupeoids, the neural spine of the second preural vertebra reaches the dorsal body outline, and has a procurrent ray (in this case, a " spine ") articulating with it. The parhypural is completely fused with the first preural centrum in *Denticeps*, but is usually autogenous in clupeoids; the condition in *Palaeodenticeps* cannot be determined.

The differences are, in my opinion, relatively slight, and in most respects are variants of the clupeoid type, variants which could be considered representative of a primitive condition. On the other hand, the loss of two uroneurals, and the presence of only five hypurals and two epurals seem to be specializations.

In most of those caudal characters in which it departs from the clupeoid condition, the denticipitid skeleton resembles that of the fossil clupeomorph genus *Diplomystus* which has a time range from Cretaceous to Eocene (Cavender, 1966; Patterson, 1967).

For example, the relationships of hypurals 1 and 2 to the first ural centrum are identical; in both taxa the first uroneural reaches the first preural centrum but is not fused with it, and the parhypural is fused with its centrum (Text-fig. 32).
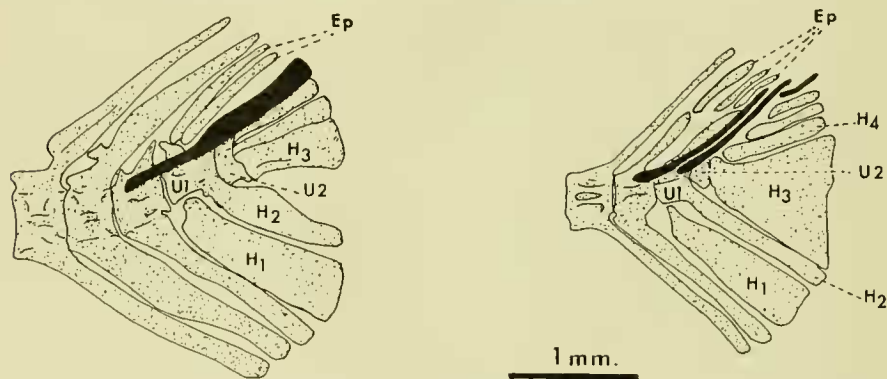

FIG. 32.   The caudal fin skeletons of : (left). *Denticeps clupeoides* and (right) *Diplomystus dentatus* (compounded from several specimens in the B.M. [N.H.]).

Differences between the denticipitid and *Diplomystus* caudal skeleton also differentiate the denticipitids from the clupeoids. Thus, the caudal skeleton of the Denticipitidae can be considered a specialized variant of the *Diplomystus* type.

Greenwood *et al.* (1966) expressed the view that the caudal skeleton of *Denticeps* ". . . approaches the condition of the elopiforms ". This view is no longer tenable. Our opinion that it is one of the most primitive types shown in living teleosts also requires some modification.

Like the *recessus lateralis*, the caudal skeleton of the Denticipitidae appears to represent, in its basic morphology, a relatively primitive state, but one still manifestly

of the clupeomorph level. Cavender (1966) seems to imply that the *Diplomystus* caudal skeleton is not of a clupeomorph type (i.e. Clupeomorpha *sensu* Greenwood *et. al.*). That there are differences will be apparent from the foregoing discussion, but that these differences can still be contained within a distinctively clupeomorph pattern should also be apparent[1].

Although the Denticipitidae possess the three major diagnostic features of the Clupeomorpha, in two of these they show a more primitive level of organization than do other living members of the superorder.

Nor are these the only characters in which the family departs from the generality of clupeomorphs. The deeply embedded scales contrast with the cauducous, flimsy scales of the clupeoid fishes, as does the complete lateral-line of the body. Both are " primitive " relative to the clupeoid condition. The simple scutes (without elongate ascending arms) appearing as folded, keeled scales and the but slightly differentiated pelvic scute (see p. 257), are not readily interpreted since both could be interpreted either as " primitive " or " derived, through reduction ". *A priori*, one is inclined to consider the condition as primitive (especially for the pelvic scute which is enlarged in the otherwise scuteless Dussumieridae; but, see Whitehead [1963b]. Yet " typical " clupeoid scutes occur in the Cretaceous *Diplomystus* species (Schaeffer, 1947).

The absence of supramaxillae in Denticipitidae is an advanced character, and one that sets the family apart from all known Clupeomorpha except the monotypic family Congothrissidae (Poll, 1964). The poorly developed coronoid process of the lower jaw is also an atypical clupeomorph condition, but one which is less easily classified in terms of specialization or primitiveness; however, a high coronoid occurs in *Diplomystus*.

The neurocranium provides several interesting problems, many of which cannot be investigated in depth because of insufficient information about the Cretaceous clupeomorphs. The extremely short parasphenoid of *Denticeps* (p. 228) is approached only by certain engraulids (*Coilia* species) amongst the living Clupeomorpha. But even in *Coilia* the parasphenoid reaches the anterior part of the basioccipital (just contacting the prootics in *Denticeps*). In other clupeoids the parasphenoid extends to below the posterior part of the basioccipital, and often to beyond the posterior margin of that bone (see Ridewood, 1905).

Denticeps also differs from all known extant clupeoids in having a tripartite occipital condyle (see p. 233). A rather similar condyle exists in *Megalops* (see p. 233) and a very similar one is found in the Jurassic elopoid *Anaethalion angustissimus* (Nybelin, 1967, pl. VIII, fig. 6). In this respect *Denticeps* must be considered primitive, but the short parasphenoid is less easily evaluated. Probably it should be considered a specialization, as should the posteriorly produced parasphenoid in those clupeoids where it extends beyond the condyle. In *Denticeps* the great enlargement of the prootic bullae (see p. 229) may be correlated with the posterior

[1] Schaeffer (1947) places *Diplomystus*, and the related *Knightia*, in the family Clupeidae, a placement accepted by Cavender (1966). From what is known about the caudal and cranial osteology of *Diplomystus* and the Clupeidae (Cavender, *op. cit.*; Patterson, 1967; Gosline, 1960; Hollister, 1936; Greenwood *et al.*, 1966) this relationship is no longer acceptable. *Diplomystus*, at least, should be accorded familial rank (less is known about *Knightia* but it should probably be kept with *Diplomystus*).

shortening of the parasphenoid; it may also be significant that in *Coilia* too the bullae are hypertrophied.

The largely cartilaginous ethmoid region of *Denticeps* is distinctive, even when compared with that region in clupeoids which also only reach a small adult size. The small size and posterior position of the vomer in *Denticeps* is approached by the Engraulidae alone amongst clupeomorphs (Ridewood, 1905; Whitehead, 1963*a*). But, even when compared to the engraulid condition, the vomer of *Denticeps* is much smaller, and little more than a flat disc of bone.

It is with the Engraulidae too that the Denticipitidae show most resemblance in cephalic lateral-line canal morphology. Among clupeomorphs (both fossil and living) only the engraulids and denticipitids have open, gutter-like supraorbital canals, bridged by bony struts, and closed by skin. In details of strut pattern, and of course in relation to the nasals anteriorly and the *recessus lateralis* posteriorly, the two families differ. This type of supraorbital canal can only be considered a specialization. Its functional significance is unknown.

The enlarged, superficially placed and complex nasals (p. 220) of the denticipitids are not encountered among any other clupeomorphs. Again, the only interpretation possible is one of specialization, possibly correlated with the open supraorbital canal system (*vide* the Notopteroidei; Greenwood, 1963).

Clausen (1959) thought that the extension of the cephalic lateral-line tubules onto operculum was ". . . an important characteristic of the family Denticipitidae . . .", and that the arrangement in *Denticeps* might be ". . . unique among teleosts, although it bears a certain resemblance to that found in Clupea (personal observation) and possibly also to that seen in some other clupeids (Berg, 1940) ". Actually, the resemblance is extremely close, differing only in minor details like the fewer ramifications of the canals in *Denticeps*. This opercular radiation of canal branches occurs, with slight variations, in all living clupeomorphs (see Whitehead, 1963*a*, and Wohlfahrt, 1937). As in the clupeoids, the canals in *Denticeps* do not house neuromasts (personal observations) but merely provide additional openings to the laterosensory system.

The hyopalatine series show a few peculiarly denticipitid characters. One of these is the spatial relationship of the metapterygoid and the hyomandibula. In all clupeoids I have examined (at least one representative of all families and subfamilies) the posterior part of the metapterygoid distinctly overlaps the hyomandibula for an appreciable distance, thereby forming a clearly circumscribed vertical pocket between the bones. The anterior margin of the pocket is closed since the metapterygoid is slightly concave in that region, and curves inwards to contact the anterior, flange-like projection of the hyomandibula.

No such pocket is formed in *Denticeps*, although there is a slight posterior overlap of the metapterygoid and hyomandibula.

These osteological differences are correlated with differences in the jaw musculature of denticipitids and clupeoids. In clupeoids (dissections were made of *Clupea harengus, Engraulis encrasicholus* and a species of *Coilia*) the *levator arcus palatini* is in two distinct parts (Text-fig. 34). The upper, and larger, originates mainly on the frontal but partly on the sphenotic (posteriorly in *Clupea* and *Engraulis*, more

anteriorly in *Coilia*); it has a narrow insertion onto the head of the hyomandibular ridge. The lower (and smaller) division has a narrower origin on the ventral face of the sphenotic. It soon broadens to insert partially on the anterior face of the hyomandibular ridge, partly around the metapterygoid lip of the pocket mentioned above, but mainly into the pocket (Text-fig. 34). Within the pocket, the muscle attaches to both the hyomandibula and the metaptergyoid. This condition was found in all the clupeoids examined.
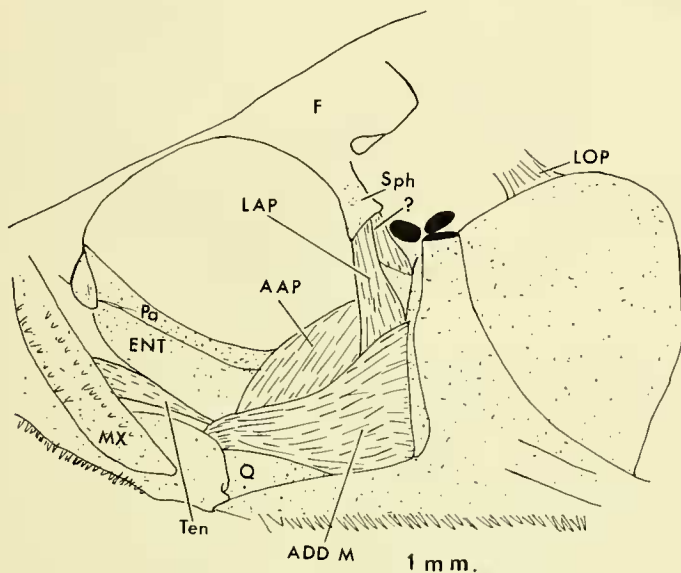
Fig. 33. *Denticeps clupeoides*. Jaw muscles. Abbreviations for muscles: AAP: adductor arcus palatini; ADDM: adductor mandibulae series; DILOP: dilatator operculae; LAP: levator arcus palatini; LAP L: lower division of levator arcus palatini; LAPU: upper division of levator arcus palatini; LOP: levator operculae; ?: possible remnant of dilatator operculae muscles. Ten: tendon. For other abbreviations see p. 216.

Denticeps shows a much simpler arrangement. There is but a single division of the *levator* muscle. It originates on the ventral face of the sphenotic, is columnar in shape, and inserts on the hyomandibula (Text-fig. 33). No trace of the large upper division seen in clupeoids could be found; presumably the *levator* in *Denticeps* is homologous with the lower *levator* division in clupeoids.

Other myological differences (Text-figs. 33 and 34) are the presence of a large *adductor arcus palatini* in *Denticeps* (where it occupies almost the posterior third of the orbit floor) and the apparent absence of this muscle in the clupeoids examined. Also apparently absent, this time in *Denticeps*, is a *dilatator operculi*; this contrasts with the extensive *dilatator* in clupeoids. *Denticeps* has, originating from the sphenotic and pterotic, a small tendinous muscle which inserts on the preoperculum

(Text-fig. 33). Since part of the *dilatator operculi* in clupeoids originates in this
area, the muscle in *Denticeps* may be its homologue.

The absence (or great reduction) of the *dilatator operculi* in *Denticeps* may be
correlated with the shape of the greatly enlarged pterotic and the resulting position
of the lateral-line openings into the *recessus lateralis*. If a *dilatator* was present it
could only lie across these openings (Text-fig. 33). In the clupeoids examined
(Text-fig. 34), despite their varied skull forms, the *recessus* openings are so situated
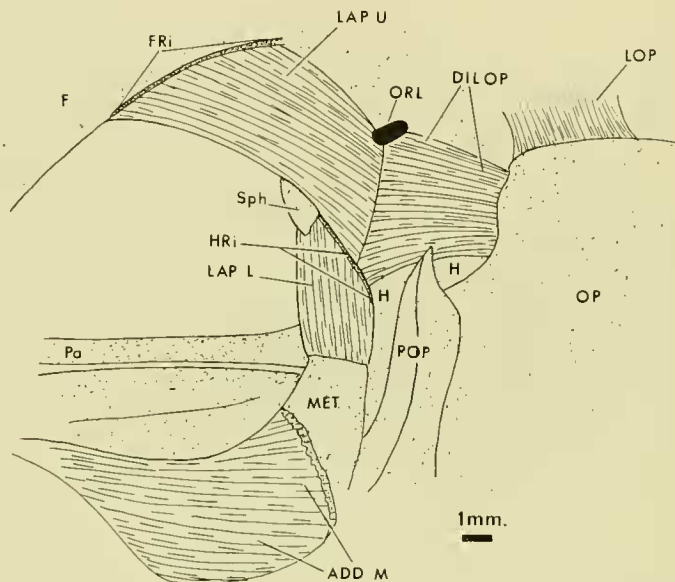

Fig. 34. *Clupea harengus.* Jaw musculature (for abbreviations see Fig. 33). The head
of the adductor mandibulae series has been dissected away to show the superficial inser-
tion of the levator arcus palatini muscle. H : Hyomandibula ; HRi : ridge on hyomandibula.

as to lie above the muscle, whose upper margin skirts the lower lip of the foramina.
(Parenthetically it may be noted that a *dilatator* fossa is present in the clupeoids,
but not in *Denticeps*.)

There are other myological differences, but these will not be discussed here.   They
do, however, reinforce the impression gained from those differences discussed above,
namely, that compared with clupeoids, the orobranchial musculature of *Denticeps*
is in part highly specialized, and in part much more primitive. Thus, for the
moment it is impossible to classify the system in *Denticeps* as more or less primitive
than the clupeoid condition.

A similar conclusion is reached when the hyobranchial skeleton is considered.
In its gross morphology, the branchial skeleton lacks the typical elongation of

individual parts which characterizes most extant clupeomorphs, and the few gill-rakers are relatively short and widely spaced. *Denticeps* also differs from most (but not all) clupeoids in having the infrapharyngobranchials well-separated in the midline (Nelson, 1967). In all these respects *Denticeps* does not show the specializations of the clupeoids.

However, *Denticeps* does show other branchial specializations seldom found in the clupeoids, namely the almost complete reduction of dermal tooth-plates associated with the hyobranchial skeleton (see Nelson, 1967; and Text-figs. 21 and 22). Only the fifth upper pharyngeal tooth-plate is present as a separate element, and there are a few teeth fused to the fifth ceratobranchial. The Pellonulinae alone among the clupeoids show a reduction approaching that of *Denticeps*, but in the pellonulines a basihyal tooth-plate is present as well (Nelson, *op. cit.*)

A reduction in the number of branchiostegal rays is considered to be a derived condition among clupeoids (Whitehead, 1963*b*.). In this respect the Denticipitidae show greater specialization than most clupeoids (p. 241). Since the number of branchiostegal rays in some *Diplomystus* species is probably about seven to ten (personal observation), the denticipitid condition is specialized in that context also.

The relatively short and simple intermuscular bones (p. 252) of the Denticipitidae, coupled with the absence of epineurals, stand in strong contrast to the situation found in extant clupeoids. On the basis of the simplicity of these bones, and especially the absence of epineurals, the denticipitid condition should be considered primitive.

Little information is available on the pectoral girdle of clupeomorph fishes, so the girdle in *Denticeps* (p. 245) cannot be evaluated fully. The scale-like postcleithra, however, seem to be outstanding and probably unique characters representing a primitive level of organization. Also at a primitive level is the double row of pectoral radials, which are otherwise only recorded in *Chirocentrus* among the extant clupeomorphs.

The pelvic plate is a baffling structure (see p. 255). I have examined the pelvic girdle in representatives of all clupeoid families, and have failed to find anything resembling a pelvic plate (*pace* Whitehead, 1963*a*). Not can I find any reference to a similar structure occurring in any other teleosts (see p. 257).

The distinctive preoperculum of the Denticipitidae is discussed above in relation to the Osteoglossomorpha (p. 261). It should probably be considered a specialized development of the *Thrissops* type, and is certainly distinctive among the Clupeomorpha.

Finally, consideration must be given to one of the most outstanding features of the Denticipitidae, the occurrence of odontodes on the roofing bones of the skull, and extraorally on the jaws (for a detailed discussion of odontodes, see Ørvig, 1967).

Clausen (1959) argues that the shape, structure and distribution of the " denticles " in *Denticeps*, together with the fact that they are attached to " . . . normal skeletal elements of the skull and pectoral girdle . . ." is indicative of a " . . . truly primitive condition . . .". As a corollary to this argument he believes that the " dermal denticles " in other teleosts (especially on the scales of siluroids and the rostrum of

the swordfish *Xiphias*) are specializations, a view generally held. Clausen's argu-
ment regarding *Denticeps* is certainly not upheld by the fossil record, and I cannot
find any other evidence to support his premises.

Consequently, I would add the occurrence of such extensive odontode patches in
Denticeps as a specialization. We have, at present, no idea of the functional
significance (if any) of the odontodes in the Denticipitidae. The proliferation of
toothlike elements outside the orobranchial cavity contrasts strongly with the
great reduction of dermal tooth-plates within the cavity (see above).

Taking into account the characters discussed, the Denticipitidae clearly stand
apart from all other living Clupeomorpha (i.e. the Clupeidae, Engraulidae, Dussu-
mieridae, Congothrissidae, Pristigasteridae and Chirocentridae of authors), and as
far as can be told, from the fossil forms as well. Yet, in a number of fundamental
characters, the family is a clupeomorph.

This departure from living forms led Greenwood *et al.* (1966) to give the
Denticipitidae subordinal status (Denticipitoidei) within the Clupeomorpha.   The
remaining extant families were grouped together in another suborder, the Clupeoidei.
Nothing has come to light in the present study that would invalidate our earlier
conclusion.

When considering the phyletic relationships of the Denticipitoidei, I have been
impressed by the relatively primitive condition of fundamental clupeomorph charac-
ters in the suborder.   The caudal skeleton has, of course, certain specialized attri-
butes (see p. 264) but it is still much less generally specialized than the clupeoid
type.   The *recessus lateralis*, by contrast, is more primitive than the clupeoid type
and does not show any peculiarly denticipitoid specialization.

On this basis I would conclude that the Denticipitoidei represent a distinct trend,
conservative in these and other characters, which split off from the clupeoid
ancestral line well back in the history of the group.   Presumably the dichotomy
occurred after the evolution of a clupeomorph type of ear-swimbladder connection
(since this is developed comparably in the two lines), and after the preliminary stages
of *recessus lateralis* development had taken place.   But, without a lot more detailed
information from the known fossil clupeomorphs (especially the *Diplomystus–
Knightia* complex), the possibility of parallel evolution of these characters cannot
be eliminated.

The presence of unique specializations in the Denticipitoidei seems to confirm
their independent trend, and perhaps reinforces the idea of a temporally distant
separation from the clupeoid stem.

Other specialized characters are shared by the Denticipitoidei and the Clupeoidei.
For instance, there is similarity in the ethmoid region of the Denticipitidae and the
Engraulidae, particularly with regard to the position and size of the vomer; again,
the two families show similarities in the organization of the supraorbital lateral-line
canal.   The short parasphenoid of *Coilia* is the nearest approach, among the
clupeoids, to the denticipitoid condition of that bone.   Loss of supramaxillae, and a
marked reduction in the number of branchiostegal rays are prominent (and restric-
ted) characters shared by the Denticipitoidei and the clupeoid family Congothrissidae.
These intergroup similarities in specialized characters would appear to be instances

of parallel evolution, because both the engraulids and the congothrissids show the unifying specializations of their suborder.

The overall relationships of the Denticipitoidei to the Clupeoidei are probably best expressed by Hennig's concept of " sister groups " (see Brundin, 1966; Hennig, 1966). Following this scheme the Denticipitoidei would be the plesiomorph (i.e. unspecialized) sister group of all other extant Clupeomorpha, which would form the apomorph (i.e. derived) sister group.

The resemblances between Denticipitoidei and Osteoglossomorpha (see p. 260) are more difficult to assess on a phyletic basis. That the characters involved are apparently derived ones, and do not, for example, appear among the living Elopoidei, is probably significant. For the moment, however, the possibility of convergence cannot be overruled. Greenwood *et al.* (1966) suggested that the fossil so-called Chirocentridae (the *Spathodactylus–Xiphactinus*, and *Thrissops–Chirocentrus* line of Bardack [1965]) might be allied to the Osteoglossomorpha. If the Clupeomorpha can be derived from a *Thrissops*-like stem, then the osteoglossomorph characters of the Denticipitidae could be explained as parallelism rather than convergence. Again, following Hennig's reasoning, the Osteoglossomorpha would be the plesio-morph sister group of the Clupeomorpha.

The idea of an osteoglossomorph–clupeomorph relationship is at the moment extremely speculative, and I mention it here simply in the hope that it may provoke further discussion. Patterson (1967) has also suggested a possible relationship between these groups, and has included the Elopomorpha in the relationship. The Denticipitoidei do not provide any evidence to support the inclusion of the Elopo-morpha.

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